Egg-size variation in North Island brown kiwi *(Apteryx mantelli)*: influences and consequences

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Abstract

Egg size in an important measure of how parents divide their investment in offspring. It has fitness consequences for both parent and offspring. Yet, significant variation in egg size is found in many avian populations and the causes and consequences of this variation are not well understood. This study examines egg size variation in a wild population of North Island brown kiwi, from Rarewarewa Reserve, central Northland, New Zealand.

My results demonstrate that in North Island brown kiwi, egg weight is a good predictor of chick hatch weight ($R^2 = 0.80$). The range of hatch weight in my study was large (254-431 g) and predicted signficant differences in both the number of days that hatchling kiwi were at risk from introduced mammalian predators and in estimated probability of survival to safe weight (>800 g). Considering both of these results, I suggest that egg weight is an important predictor of lifetime fitness in North Island brown kiwi.

Assortative mating is a pattern of mating where certain individuals, with particular traits, pair more often than would be expected under random pairing. Using measures of adult bill length and body weight, I could find no evidence of assortative mating in North Island brown kiwi.

Eggs in my study population ranged in estimated fresh weight from 317-551 g (n = 496), with a mean of 445 ± 45 g (± SD). Egg weight had a high degree of repeatability (R = 0.67) for individuals. Factors that did a good job of explaining fresh egg weight, and were included in all 6 top models, were male body weight, female body weight, and site. Also included in some top models was clutch size (3 models), male bill length (2 models), and sequence of egg in year (2 models). Male and female body weight had a strong positive association with egg weight, whilst the effect of male bill length and clutch size was weak and negative.

Egg weight did vary across metrics such as clutch size, sequence of egg in a year, or nest in year. This has relevance to conservation breeding programmes such as Operation Nest Egg, which takes wild kiwi eggs away from parents for incubation in captivity thus encouraging birds to lay replacement clutches, as it provides evidence that female kiwi do not respond to the pressure of having to lay more eggs by making later ones smaller.

Acknowledgements

Thanks firstly to my supervisory team (Dave Kelly, Hugh Robertson, and Jim Briskie) for giving me continual support and guidance throughout this daunting process. Special thanks to my senior supervisor Dave, for always being available with useful advice, even after the millionth time arriving at his office door unannounced. Thank you to all the Department of Conservation staff, volunteers, and dogs who chased kiwi around Northland forests to collect these data.

Thanks to Mum and Dad for giving birth to me, and disproving the many theories of parental investment versus clutch size trade-offs that I am about to discuss. Also to Leslie for being my second mother.

Thanks to Sam, Dayna, and Theo for opening their home to me and providing welcome distractions to the stresses of university life. Theo; *woof bork snoot n' boop.*

The enormous size of the Kiwi's egg has often been the subject of speculation and comment; for, till the fact was established beyond all question, it seemed almost impossible that the very large eggs occasionally brought in by the natives were the produce of this bird.

Sir Walter Lawry Buller, 1888

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1 Introduction

In this thesis I explore the causes and consequences of variation in egg size of a population of North Island brown kiwi (*Apteryx mantelli*) from Rarewarewa Reserve in Northland, New Zealand. Egg size variation of North Island brown kiwi is interesting because kiwi (Apterygiformes) are highly unusual among birds in a number of reproductive and physiological traits, and because their populations are intensively managed due to their declining populations. Questions remain as to the cause and consequence of egg size variation in kiwi, as well as whether breeding management programmes are having negative effects on parent kiwi.

1.1 General life histories

The fitness of an individual can be defined as the number of its offspring that reach reproductive maturity. These offspring must be well provisioned to survive against the environment, competition, and predation until they reach an age where they themselves can reproduce and thus the cycle starts again. These patterns of investment which increase the offspring's chance of surviving (and thus reproductive success) can be termed "parental investment" (Trivers 1972), and can affect propagule size, propagule number, and distribution in time and space. If offspring fitness was independent of offspring size, the optimal strategy would be to minimise size and maximise number of offspring (Brockelman 1975). However, if offspring fitness increases with size, we might expect that offspring would be larger and fewer (Lloyd 1987). As Trivers (1972) stated, it can be useful to think of each offspring as independent investment units. Increasing investment in one offspring tends to decrease investment in others. Natural selection results in the optimal balance in reproductive traits between the benefits and costs of current reproduction versus future reproduction (Heath et al. 1999). As reproductive traits are a key determinant of fitness, I expect these to undergo intense selection.

When describing the amount of investment parents provide their offspring, egg size is an important measure as it strongly affects both parental and offspring fitness (Bernardo 1996; Ardia et al. 2006). Larger eggs almost certainly have increased costs to parents, though the physiological mechanisms (e.g. protein limitation, immuno-deficiency) which mediate these costs are unclear (Williams 2005). Increased yolk reserves of larger eggs are positively associated with hatchling size and growth (Rahn et al. 1975). Considering

the strong selective pressures that must control egg size, it is curious that large variation in egg size (weight and/or volume) has been reported within and between a diverse range of taxonomic groups, including fish (Ware 1975; Hutchings 1991; Beacham & Murray 1993; Einum & Fleming 2002), turtles (Karen A. Bjornal; & Carr 1989; Rowe 1994; Wilkinson et al. 2005), snakes (Roosenburg & Dunham 1997; Ji et al. 2009), and birds (see review by Christians 2002). In avian species, the largest egg in a population is generally at least 50% bigger, and sometimes 200% bigger than the smallest egg (Christians 2002).

Egg size is also an important measure of egg quality, as it reflects the quantity of yolk reserves available for embryo and chick development (Bolton 1991; Ardia et al. 2006). Larger eggs tend to have higher hatching success (Perrins 1996) and lead to larger hatchlings and faster growth (Hipfner & Gaston 1999). A strong positive relationship between egg size and initial hatch size for both skeletal dimensions and weight of chicks has been reported in many avian species (e.g. Ricklefs et al. 1978; Wilson 1991; Grant 2008). A similar relationship has also been reported between hatch weight of chicks and survival (Williams 1994; Blomqvist et al. 1997). Though some studies have suggested that parental quality (which is positively correlated to egg size) may have a significant role to play in determining chick survival (Bolton 1991), these conclusions probably do not have the same relevance to precocial species which provide less parental care and thus are much more dependent on pre-hatching parental investment (incubation length and egg size). Nevertheless, the confounding effect of parental quality and egg size is an important consideration.

Most of the variation (~70%) in egg weight of avian species is explained between clutches (Christians 2002), leaving ~30% of the variation due to within-clutch differences. It is not clear whether intra-clutch egg size variation is adaptive (Slagsvold et al. 1984; Williams et al. 1993), a constraint (Arnold 1991; Nilsson & Svensson 1993; Kilpi et al. 1996) or both (Vinuela 1997; Aparicio 1999). In other words, questions remain as to whether the differences in egg size within a clutch is beneficial or simply a limit of egg production. Proponents of the adaptive viewpoint suggest two strategies birds may employ to maximise fitness: (1) "brood-reduction" in birds with a smaller final egg, and "brood-survival" in birds with a larger final egg (Slagsvold et al. 1984). These strategies relate to the size disadvantage that the last-laid egg has compared to its siblings in species with asynchronous hatching. The "brood-reduction strategy" allows parents to adjust the number of offspring they raise in relation to prevailing

environmental conditions at the nestling stage, whereas the "brood-survival strategy" improves the last-laid egg's chance of survival to match its siblings (Slagsvold et al. 1984). Conversely, proponents of the constraint viewpoint suggest that the adaptive hypotheses are too simplistic, because these ignore evidence which shows many bird species' first laid-egg actually having the most variation in relative size, and species with precocial young (which have synchronous hatching and low levels of intra-brood competition) exhibit intra-clutch egg size variation (Arnold 1991), evidence which opposes the adaptive viewpoint. The suggested constraint mechanisms mainly center on resource limitations. For example, Kilpi (1996) suggests that intra-clutch egg size variation in the Herring Gull *(Larus argentatus)* is mainly a non-adaptive response to poor resource availability during egg laying, and thus a constraint. Though authors often suggest resource limitation as an explanation for intra-clutch egg size variation, Williams (2005) points out that we actually know relatively little about the costs of egg production, or even if they are resource-based costs.

Considering the large amount of variation explained by inter-clutch differences, egg size appears to be a characteristic trait of individuals, though the particular traits that determine egg size are unclear (Williams 2005). Egg size is often highly consistent within individuals between breeding attempts (high repeatability), and highly consistent due to additive genetic variance (high heritability) (Lessells et al. 1989; Falconer & Mackay 1996; Christians 2002). Supplemental food, dietary supplements (protein and/or calcium, which are commonly cited as egg-production limiting factors) and ambient temperature during egg formation explain a relatively small amount of the variation in egg size (Christians 2002), indicating the importance of individual variability. Female mass or size rarely explains more than 20% of the egg size variation within avian species (Christians 2002), however in non-avian species, especially fish (Heath et al. 1999; Johnston & Leggett 2002) and turtles (Morse & Schmitt 1985; Bjorndal & Carr 1989), female mass or size has been found to explain a substantial proportion ($> 20\%$) of egg size variation.

Strategies of when to provide investment (pre-hatching versus post-hatching) to their offspring varies between species. These strategies fall along an altricial-precocial spectrum (Figure 1.1), which describes the stage of development at hatching. Oken (1837) said of altricial birds; "they come naked and blind into the world, needing to be fed in the nest" and of precocial birds; "the young come from the egg with sight and feathered, not being fed, but soon running about and searching for their food by

themselves". For altricial offspring, parents divide their investment both pre- and post-hatching. Pre-hatching investment includes such things as egg quality, egg size, and incubation quality. Post-hatching investment includes such things as nest supervision, supplemental feeding, and predator deterrence. Parents of precocial offspring are taking a risk that their offspring will be able to survive independently, so there is selection on parents to better provision offspring so they are well developed at hatching.

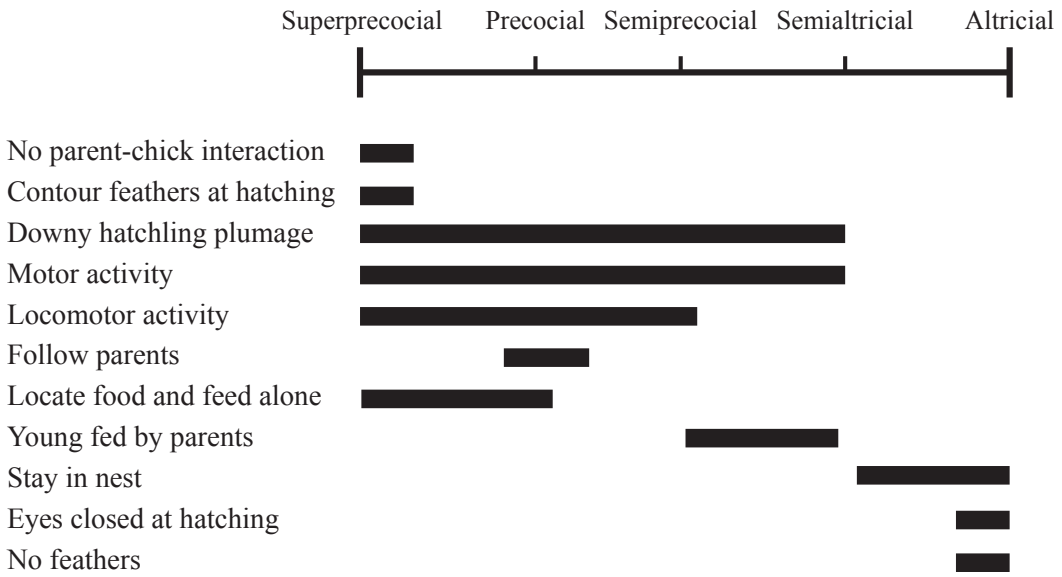

Figure 1.1: Patterns of avian development according to the precocial-altricial spectrum. Adapted from Starck & Ricklefs (1998).

Egg sizes in altricial species are generally smaller and have a lower energetic cost compared to precocial species (Masters-Vleck et al. 1980). This is because altricial hatchlings rely on their parents for provisioning so do not need to be as well developed at hatching. Precocial hatchlings retain more yolk after hatching than altricial hatchlings because they are not fed by their parents and need to independently meet their nutritional requirements (Masters-Vleck et al. 1980), which necessitates large calorific contents of eggs.

The length of the incubation period of bird eggs is strongly and positively correlated with egg size (Rahn & Ar 1974; Boersma 1982), though interspecific variability is much greater than intraspecific (Nice 1954). Interspecific differences in incubation period are

likely to reflect ultimate mechanisms such as parental investment strategies, whereas intraspecific differences can largely be attributed to proximate mechanisms such as season, weather, and parental attentiveness (Nice 1954; Drent 1967; Boersma 1982). Many avian species lose significant amounts of weight during incubation due to changes in the regulation of energy balance, rather than low food availability (Sherry et al. 1980). The controlled loss of weight makes possible types of reproduction which may incur restricted food access (Sherry et al. 1980), but birds subsequently recover in the non-breeding season (Williams 2005). If larger eggs require longer incubation, and longer incubation results in larger weight losses for parents, there would be a selective benefit for parents of large eggs to be large themselves; in order to mitigate the impact of the weight loss.

Assortative mating is a pattern of mating where individuals pair with other individuals, with certain characters, more often than would be expected under random pairing. Relevant characters could include age, body size, or plumage colouration. In assessing assortative mating it is interesting to quantify the magnitude and direction of sexual size dimorphism, because this highlights attractive traits and the reason why dimorphism evolved in a population could be the same reason why a population should be expected to assortatively mate. Evidence of *positive* assortative mating (similar pairings) has been found in many sexually dimorphic bird species (Coulter 1986; Groth 1993; Freeberg 1996; Wagner 1999; Delestrade 2001; MacDougall & Montgomerie 2003; Helfenstein et al. 2004), but less conclusive evidence has been found for reversed size dimorphism (female larger than male) bird species (Mueller 1992; Warkentin & James 1992). It has been suggested that if assortative mating were to occur in reversed size dimorphism species, it would be in the *negative* direction (dissimilar pairings) (Olsen & Olsen 1987; Sandercock 1998).

Three popular groups of hypotheses (see review by Mueller & Meyer (1985)) have been proposed to explain the evolution of sexual size dimorphism in birds: (1) sexual selection, (2) intersexual competition, and (3) ecological role division, but the evolutionary origin of RSD remains unclear (Mueller 1986; Mueller 1989; Sandercock 1998). Conclusive evidence (or even convincing hypotheses) regarding the evolution of RSD are lacking, with oft-quoted mechanisms having little relevance to disparate taxonomic groups. For example, aerial agility (which increases with decreasing isometric size) is a popular hypothesis for why males could be selected to be smaller (Mueller 1986; Blomqvist et al. 1997; Catry et al. 1999; Sandercock 2001) but this makes no sense for flightless species.

The aerial agility hypothesis falls in the sexual selection grouping, because it assumes that females choose partners based on aerial displays. Another example is the prey-size hypothesis that proposes that inter-sexual competition would be reduced if members of different sexes tended to take different sizes of prey. Prey-selection could however be a result of RSD, rather than the cause (Longland 1989). Of course, a single general answer to the evolution of RSD is not neccessary if it is assumed that RSD evolved independantly in the four distantly related avian orders which exhibit RSD (Longland 1989).

1.2 The biology of kiwi

Kiwi (Apterygidae) are an ancient family of flightless, mainly nocturnal, ratites endemic to New Zealand. Five species of kiwi are currently recognised from two primary morphological groups (Shepherd & Lambert 2006). The brown kiwi morphological group comprises North Island brown kiwi (*Apteryx mantelli*), rowi (*Apteryx rowi*), and tokoeka (*Apteryx australis*). The spotted kiwi morphological group comprises great spotted kiwi (*Apteryx haastii*), and little spotted kiwi (*Apteryx owenii*). The 'brown' and 'spotted' terms are in reference to the two types of kiwi plumage (Figure 1.2); with brown kiwi taxa having feathers streaked brown, grey, and/or black length-ways, but spotted kiwi taxa have grey transversely barred pale and darker feathers (Tennyson et al. 2003). This thesis focuses on North Island brown kiwi.

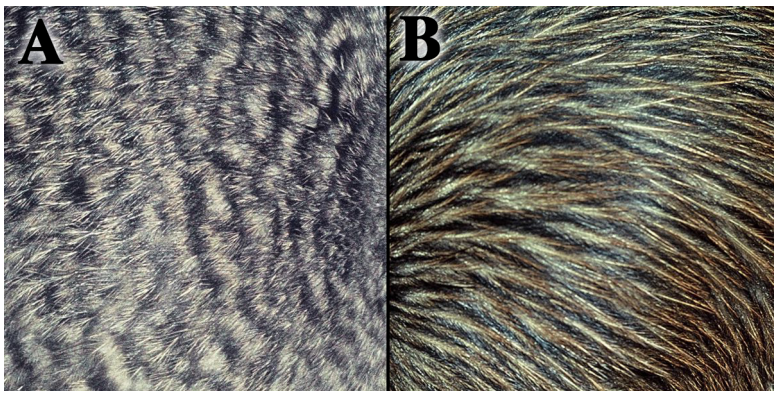

Figure 1.2: Plumage differences of the two morphological groups of kiwi; spotted kiwi (A) and brown kiwi (B).

North Island brown kiwi are one of four kiwi species that are classified as 'threatened' (Miskelly et al. 2008). The fifth kiwi species, little spotted kiwi, is classified as 'at risk', largely due to a number of population strongholds on managed offshore islands (Colbourne & Robertson 1997). Kiwi have dramatically declined in range (Figure 1.3) and abundance since New Zealand's settlement by Polynesians and Europeans (McLennan et al. 1996). In mainland North Island forests, kiwi abundance has declined by at least 90% over the last century (McLennan et al. 1996) and mainland populations contain significantly fewer juveniles than similar populations on predator-free offshore islands (Colbourne 1992). A 1996 estimate found North Island brown kiwi were declining at a rate of 5.8% per annum (McLennan et al. 1996). Introduced predators including cats (*Felis catus*), dogs (*Canis familiaris*), ferrets (*Mustela furo*), pigs (*Sus scrofa*), possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), and weasels (*Mustela nivalis*) are the main factor causing the decline of kiwi in mainland populations (Diamond & Veitch 1981; McLennan et al. 1996). Loss of habitat from large areas of forest and scrub land being converted into pastoral farmland also would have had a impact on kiwi populations (Blue & Blunden 2010), though large-scale land conversions have now mostly halted.

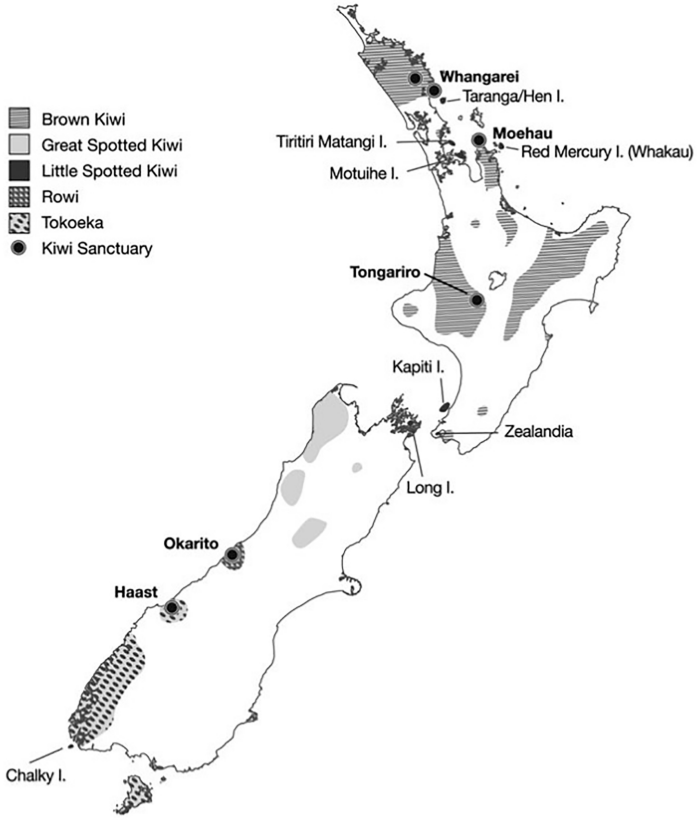

Figure 1.3: Distribution of the five species of kiwi in New Zealand and the location of the five Kiwi Sanctuaries (bold circles). Note that the Whangarei Kiwi Sanctuary has two separate blocks. From Robertson et al. (2012).

Mortality risk is not constant throughout the life of kiwi, and the main predators of each life stage also change (Figure 1.4). Adult kiwi mortality is relatively low (5%-16% per annum), because adult kiwi are large enough to defend themselves against all the common mammalian predators (McLennan et al. 1996). North Island brown kiwi reach a critical safe weight (800 g) 3-4 months after hatching, when they become able to fight off cats, possums and stoats. In contrast, kiwi chicks are highly susceptible to predation, especially from mustelids. It is estimated that 94% of juvenile North Island brown kiwi do not reach adulthood, largely due to predation (McLennan et al. 1996). Mammalian predators (especially possums) are responsible for kiwi egg losses. In one study of North Island mainland forests (McLennan et al. 1996), it was found that whilst predators eating eggs directly is relatively rare (2% of egg losses), predators causing nest desertion by parents and subsequent egg death (10%-20% of egg losses) was of much more impact.

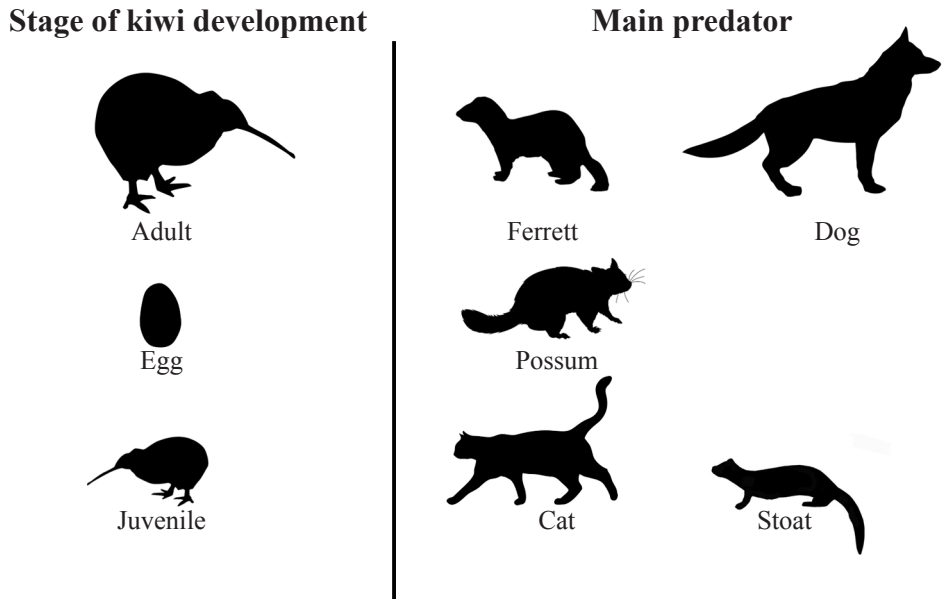

Figure 1.4: The main predators of North Island brown kiwi change throughout their life stage.

North Island brown kiwi are generally monogamous with long-term pair bonds (McLennan 1988; Taborsky & Taborsky 1991; Taborsky & Taborsky 1999). Social and genetic monogamy is prevalent even in male sex biased populations, with extra-pair copulation rare (Taborsky & Taborsky 1999). This, combined with the large overlap between paired females' territories and the range of unpaired males indicates that the environmental potential for polygamy (EPP) hypothesis is insufficient to explain the mating system of kiwi (Taborsky & Taborsky 1999). Male kiwi should ensure their partner's fidelity because of their enormous incubation investment (male North Island brown kiwi provide all the incubation (McLennan 1988)). They do this by mate-guarding during their partners' fertile period, but females could possibly produce extra-pairings whilst males are incubating (when mate-guarding is not possible). However, little evidence of extra-pairings has been found (Taborsky & Taborsky 1999). So what then explains the high degree of monogamy observed in kiwi populations? Tarborsky (1999) suggests the parental limitation hypothesis, that is, the high cost of egg production means that females are energetically constrained from mating with additional partners.

Due to their threatened status and declining population, North Island brown kiwi have been experimentally managed in central Northland using four main strategies by the

Department of Conservation (Robertson et al. 2011);

1. Unmanaged - doing nothing.
2. Trapping - laying kill, cage, and leghold traps for mustelids, cats, and possums.
3. Poisoning - ground and aerial poisoning using 1080 (sodium monofluoroacetate), brodifacoum, cholecalciferol, and/or cyanide to kill mammalian pests.
4. Operation Nest Egg (ONE) - as described below.

Successful management at some sites has led to population stablisation and increases (Robertson et al. 2011). Adult survivorship was the same across all four management techniques (92.7% per annum), whilst chick survival (10 - 183 days) was low under unmanaged (11.1%), poisoning (32.6%), and trapping (14.7%) but high under ONE (86.9%) (Robertson et al. 2011). It has recently come to light that periodic poisoning must accompany trapping, in order to kill 'untrappable' stoats which become trap shy and avoid going into traps (Robertson et al. 2016).

One of the most successful strategies in North Island brown kiwi management has been ONE, which generally operates as follows (Colbourne et al. 2005):

1. Kiwi eggs are removed from wild nests. Eggs should be more than 20 days old at removal, as eggs younger than 10 days old have not been able to be successfully hatched in captivity. If nests are accidentally disturbed in the wild then eggs of any age can be collected. In brown kiwi, to balance the risk of predation, nest desertion, and successfully hatching captive eggs, collection is aimed for when the oldest egg is 60 days old and younger egg in a two-egg clutch is at least 30 days old.

2. Whether eggs are collected during day or night appears to have no effect on hatching rates. But incubating males may be more aggressive during the daytime, lashing out and possibly puncturing or cracking eggs.

3. Eggs are generally transported to the incubation facility within 8 hours, although sometimes held overnight in emergency incubators. Jarring was recorded during a typical transport operation and found to be lower than the threshold for damage to emu eggs. Protocol dictates that eggs are to be transported in chilly-bins lined with shredded paper.

4. Optimum incubation temperature has been found to be 34-37°C, and if temperatures are too low or too high developmental problems can occur in chicks.

Humidity also needs to be controlled to ensure a daily weight loss of 0.7-1.2 g.

5. Very few wild kiwi chicks die during the natural hatching process, although it is not known what assistance kiwi parents provide. Most eggs in captivity hatch without needing assistance, but occasionally chicks are not able to free themselves and staff have to intervene. Early intervention does not seem to cause any further issues for the chicks.

6. After hatching, chicks are carefully monitored to ensure healthy weight gain. If unhealthy weight gains are recorded, veterinary intervention is provided (10% of chicks). Failure to completely absorb the yolk sac, and coccidiosis were the main causes of death of chicks. Implementation of strict hygiene procedures mostly eliminated the latter.

7. Hatched chicks are transferred to outdoor pens or crèche islands once 3-6 weeks old, and generally have good survival rates. Transferring chicks at less than 40 days old saves cost of feeding captive birds and reduces the risk of disease.

8. Once kiwi sub-adults are at least 7 months old, and weigh over 1200 g they are eligible for transfer back to the mainland. Mortality in the month after release has been high, mainly due to kiwi choosing inappropriate daytime roosts. Survival of island-reared kiwi has been recorded to be higher than captive-reared birds, possibly due to better adaptation to life in the wild. Most kiwi are in good condition at release.

In Northland, the success of eggs hatching under ONE is 62% compared with unmanaged nests, 52%. The survival rate per annum of chicks to 6 months old in captivity or island crèches (81%) far exceeds unmanaged areas (11%). The 81% survival rate also far exceeds the 20% survival rate estimated to be required to sustain mainland populations (Colbourne et al. 2005).

Best practice protocols have already been written for the ONE program (Colbourne et al. 2005), but refinements are constantly being made through careful monitoring of the fate and reproductive output of ONE birds. The results of this thesis research could potentially inform these best practice protocols, especially if it was found that the egg removal regime was causing significant harm to female kiwi due to forced renesting increasing yearly egg production costs.

1.3 Aims

1. Determine the fitness effects of egg size in North Island brown kiwi
    - Determine the general relationship between egg size and chick size
    - Determine specific factors that affect the chick / egg size ratio (variation from general relationship)
    - Determine relationship between chick size and survival.
2. Describe general assortative mating pattern of North Island brown kiwi
3. Determine best predictors of egg size of North Island brown kiwi
    - Determine significance of female size
    - Determine significance of male size
    - Determine significance of other covariates: laying date, laying sequence, and clutch size.

1.4 General methods

1.4.1 Source dataset

I was supplied a dataset to analyse for my thesis by Hugh Robertson at the Department of Conservation. Data on the breeding ecology of radio-tagged kiwi was collected over 17 breeding seasons from 1994-2011 as part of a long-term conservation management programme for North Island brown kiwi in central Northland, New Zealand.

1.4.2 Study area

The study was carried out in four patches (Purua, Rarewarewa, Riponui, and Hodge's Bush) of remnant broadleaf-podocarp forest within 5 km of Rarewarewa Reserve (35°37'S, 174°08'E) in central Northland, New Zealand (Figure 1.5).

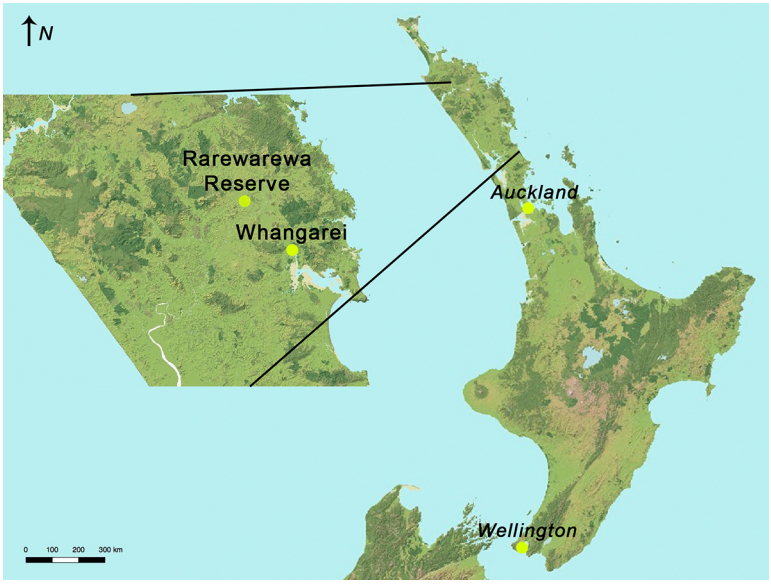

Figure 1.5: Location of Rarewarewa reserve study site in Northland, New Zealand.

Northland has a subtropical oceanic climate, with warm humid summers and mild wet winters (Metservice 2018). Mean summer temperature in Whangarei, 30 km away, is 19.4°C and mean winter temperature is 11.7°C. On average, there was 1950 sunshine hours each year. Annual rainfall at Otakairangi, within the study area, from 1993 to 2010 was 1323 mm (range 1109 to 1729 mm). Most rain fell during late autumn and winter months (May to July), but in summer and autumn tropical storms sometimes brought high winds and heavy rainfall from the east or northeast.

1.4.3 Site descriptions

The forest patches ranged from 35-110 ha, though some kiwi also resided in adjacent patches of exotic conifer woodlots or scattered native forest fragments in nearby farmland, and some nests were on hillsides in surrounding pasture. Two blocks, Purua (110 ha) and Rarewarewa (55 ha) were centered on old volcanic cones (387 m and 365 m elevation respectively), Riponui (45 ha) was on the southern side of a low ridge and deeply incised by a series of parallel streams, and Hodge's Bush (35 ha) was in a broad south-facing basin and valley. The main canopy tree in all four forest patches was tararire *Beilschmedia taraire*, with lesser amounts of towai *Weinmannia silvicola*, kohekohe *Dysoxlyum spectabile*, hinau *Eleaocaprus dentatus*, karaka *Corynocarpus laevigatus* and puriri *Vitex lucens*. A few emergent totara *Podocarpus totara*, rimu *Dacrycarpus*

dacrydioides and kauri *Agathis australis* had escaped being logged in the early 1900s, and there were still many old stumps from logged trees and the occasional felled tree trunk that had been left behind. Ground cover varied from minimal in Hodge's Bush that was grazed until the late 1990s, to heavily overgrown with parataniwha *Elatostema rugosum*, kiekie *Freycinetia banksii*, supplejack vine *Ripogonum scandens*, and ferns in damp gullies and faces of the other three forest patches. Inside the fenced margins of the forest blocks were small areas of rank grass, rushes, Mexican devil *Ageratina adenophora*, mistflower *A. riparia* and blackberry *Rubus* spp.

1.4.4 Data collection

Birds were caught after being located by dogs trained especially to find and indicate the location of kiwi in their daytime dens (Robertson & Fraser 2009). The birds were usually sheltering in a short burrow, hollow log, fallen clump of the epiphyte *Astelia*, under the bole of a fallen frond of nikau palm *Rhopalostylis sapida*, or under dense vegetation.

A total of 166 different adult males were fitted with a 25g Sirtrack® 2-stage radio-transmitter between 3 January 1994 and 31 December 2011, for a total of 823 bird-years, spread over 188 different tracking periods ranging from 8 days to 6363 days (17.4 years). The transmitter was attached to the tibia with a hospital identification bracelet and electrical tape (Miles & McLennan 1998) so that their nests could be located. The transmitters were checked approximately every 6 months to ensure that they were not too tight in accordance with best practice procedures (Robertson et al. 2003), and then replaced and switched to the opposite leg every 12-14 months. Since about 2006, "Sirtrack egg-timer" or "Sirtrack chick timer" transmitters were used because these provided a series of radio pulses that indicated the time elapsed since incubation began, or since eggs hatched, based on changes in the movement patterns of the males.

In total 73 adult females were radio-tagged for a combined 148.0 years in 95 separate tracking periods ranging from 1 day to 5499 days (15.1 years) to determine their territory, locate their partner when they were sharing a daytime den, and to determine their survival rate relative to that of males. Unless otherwise specified, analyses of breeding ecology were restricted to the breeding efforts associated with radio-tagged males that were followed throughout a complete breeding season.

Males were checked about once every 3 weeks and any likely nest was marked with tape on a nearby tree. The typical gap between hatching of chicks in the same clutch, and bill and weight measurements provided a guide to ageing older nestlings, because kiwi chicks lose weight for the first 10-15 days, before regaining their hatching weight at about 20- 30 days old. Approximate laying dates were determined as the most parsimonious fit based on egg-timer records, and/or estimated hatching date from the age of chicks minus 80 days for first eggs in a 2-egg clutch and 75 days for second eggs in a 2-egg clutch and eggs in a 1-egg clutch, and allowing about 23 days between eggs. When no chicks hatched, the estimated first egg date was the midpoint between when the male was first on the nest and its previous record.

Nestlings were marked permanently with a uniquely numbered wing-tag, or with a Trovan® transponder injected subcutaneously above the ribcage. Most chicks were also fitted with a miniature (9g) single-stage radio- transmitter, attached with a cut-down identification bracelet and electrical tape, so their fate could be determined (Robertson et al. 2011).

The four study sites were used for studies of the incubation behaviour of brown kiwi (Colbourne 2002) and for the initial development of Operation Nest Egg (ONE). These projects provided opportunities to collect data on egg and chick measurements, and the hatching interval between eggs in the same clutch. These measures would have been hard to obtain in the wild without risking nest desertion.

1.4.5 Data analysis

All data analysis was conducted using R version 3.4.0 and RStudio version 1.1. Linear models were fitted using the base `lm` function. Generalised linear mixed models were fitted using the `lmer` function in the `lme4` package. I have often used the `tidyverse` ecosystem of packages, which work in common because they all share a common 'tidy' data structure. Data manipulation utilised the `dplyr` package which employs a flexible 'grammar of data manipulation' approach. Likewise, plotting used the `ggplot2` package which employs a 'grammar of graphics' approach.

The formatting and production of this thesis used LaTeX, R Markdown and `knitr` which encouraged reproducible research methods, and are all free open-source software.

2 Fitness effects of egg size: why do big eggs even matter?

2.1 Introduction

It has been well known, for at least one hundred years, that large eggs produce large chicks (Halbersleben & Mussehl 1922). At least, this is well known for commonly studied species such as domestic fowl. Chick size as a predictor of post-hatching development and survival is also well established in many domestic and wild species (Galbraith 1988; Williams 1994; Grant 2008), but little evidence is available in the literature for kiwi species. Kiwi egg size relationships have had comparatively little attention, which my thesis aims to address.

Egg production is almost certainly costly for parents (Williams 2005), and parents face a trade-off between offspring quality and quantity (Lack 1967). Why then are kiwi eggs so large? Much larger in fact than would be expected under typical allometric relationships (Calder 1979). In this chapter I intend to describe the fitness benefits for juvenile kiwi in coming from large eggs, in terms of reduced predation during the riskiest period of their lives, and thus increased lifetime fitness and survival.

Kiwi evolved largely in the absence of mammalian predators, but now face a suite of carnivores introduced by Polynesians and Europeans (Diamond & Veitch 1981; McLennan et al. 1996; Basse et al. 1999). Their lack of defensive mechanisms has led to population size declines and range reductions. The survival of adult kiwi (2-3 kg) is generally high as they are large enough to defend against rats (*Rattus* spp.) and stoats (*Mustela erminea*). They are still vulnerable attacks by dogs (*Canis familiaris*) and ferrets (*M. furo*) (McLennan et al. 2004), though these types of attack are relatively rare. Young kiwi are the most vulnerable to predation, especially from stoats, until they reach about 800 g (McLennan et al. 2004) at 97-166 days of age (Figure 2.1). Once over 800 g they are not entirely safe from predators, but the risk is much lower for the rest of their lives.

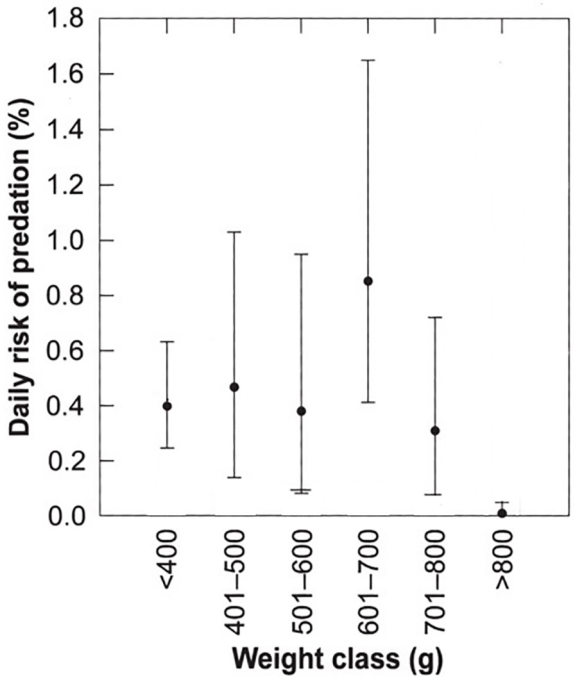

Figure 2.1: Daily mortality rates of North Island brown kiwi in a wild Lake Waikaremoana population. Mean with 95 percent confidence intervals (from McLennan 2004).

Most kiwi chicks are super-precocial, which means that parents do not provide care or resources for their young after hatching (see Chapter 1 for more on precociality). Chicks hatch with full adult plumage, good eyesight (Howland et al. 1992) and mobility. Remaining egg yolk stores provide nourishment for the first few days after hatching (Calder 1979; McLennan 1988), then chicks begin independently foraging away from their nest within 10 days (McLennan 1988). The long incubation period and large egg size are key features of their precocial strategy. For a precocial bird like the kiwi, all of the resources parents give to their offspring are given pre-hatching as either genetic material, egg contents, or incubation (rather than post-hatching care or feeding).

Young kiwi gain weight at an exceptionally slow rate. Juveniles take at least 880 days to reach adult size, which is about four times longer than would be expected for an otherwise equivalent 2-3 kg bird (McLennan et al. 2004). It has been suggested that this slow rate of development is due to a long history of resource limitation and has been viable due to a lack of predators (McLennan et al. 2004). Too fast development can lead to limb deformities in kiwi and other precocial birds (Prier et al. 2013). Slow rate weight gain is however associated with poor juvenile survival in the presence of

introduced predators (McLennan et al. 2004). The slow growth of kiwi (possibly in response to resource limitation) has developed over a long history, and is in contrast to the relatively recent pressure to hasten growth to avoid predation from introduced mammals.

In this chapter I aimed to determine the fitness effects of egg size in a population of North Island brown kiwi from Rarewarewa Reserve, Northland, New Zealand. I achieved this by firstly quantifying the relationship between egg size and chick size (at hatching), which was expected to be a strong positive relationship. I also tested whether other factors such as female bill length and female body weight (both reasonable uni-variate measures of avian body size), time of year (kiwi show strong seasonal distribution in egg laying), or shape of egg (which would affect fresh weight estimation) would affect this relationship. Then I estimated the fitness effects of increased chick size, which was expected to be a strong positive relationship in wild populations due to the weight-dependent risk of predation from introduced mammals. Once both of these relationships were determined it would be possible to draw a logical conclusion between them (e.g. large eggs result in large chicks whom have high survival and thus increased lifetime fitness).

2.2 Methods

2.2.1 Estimating fresh weight of eggs

A key measurement for the analysis of this chapter was egg weight, but this varies over time for an individual egg. I had been provided egg weight and dimensions (length, width) for the North Island brown kiwi eggs, but these had been taken at various times depending on when the field workers had found or collected the eggs. Bird eggs are known to lose weight throughout incubation due to the loss of water (Rahn & Ar 1974), but egg dimensions are fixed. A standardised measure of egg weight was necessary to make comparisons between eggs in our dataset, and the best baseline would be egg weight at time of laying (fresh egg weight), so I estimated fresh egg weight for all 496 eggs in my dataset. Fresh egg weight is often estimated from egg dimensions with good accuracy (Carter 1975; Reid 1981) using a methodology described by Hoyt (1979):

$$W = K_w L B^2 \quad (1)$$

Where W = fresh weight (g), L = length (mm), B = breadth (mm) or maximum diameter (mm). K_w (g/mm^2) is a species-specific weight coefficient which is essentially density (weight per volume).

Hoyt (1979) provided a species-general K_w constant derived from 26 diverse bird species of 0.548 (g/mm^2) ± 0.016 (Hoyt 1979). Kiwi are unusual in regards to many aspects of their breeding physiology so determining K_w for my study species would improve the estimates of fresh egg weight. A study that used mostly captive-laid brown kiwi eggs found K_w to be 0.565 (g/mm^2) (Reid 1981). Captive-laid eggs are known to be a slightly different shape than wild-laid eggs, which may alter the K_w between these two types of eggs. For my study population K_w was calculated by Robertson (unpublished data) using 27 freshly laid eggs to be 0.5616 (g/mm^2) ± 0.0087. I have used this value for fresh egg weight estimation.

2.2.2 Statistical analysis

I had data on 496 eggs, and for 111 of these I also had chick hatch weight, so I built a statistical model to predict chick weight. A linear model was fitted using least-squares regression in `R` version 3.4.0. Chick weight was set as the response variable and various explanatory variables were tested in separate independent models. These explanatory variables were: egg weight, day of the year laid, shape (length:diameter ratio), female bill length, female non-gravid weight (body weight measured when not pregnant so egg weight would not be included). The identification of parents to each egg was determined by field workers: the male parent was always assumed to be the bird incubating an egg, and the female parent was assumed to be the female socially associated with a male during the mating period (see Taborsky (1991) for full details of kiwi mate guarding). Measures of non-gravid weight and bill length were long term averages for individual birds. For models which included female size variables I used a generalised linear mixed model from the `lmer` package, with a random term for female identity. As in some cases there was multiple eggs from the same female in the dataset, the egg weights were not all independent from each other, so the use of a mixed model corrected for the structure of the dataset.

All of the explantory variables were also tested together in a multiple linear regression mixed effects models, fitted using the `lmer` package, with a random term for female identity.

2.2.3 Chick growth rate

I did not have information on the growth rates of chicks in this particular study population. In any case, growth rates of chicks raised in captivity, using standard techniques such as supplemental feeding, would have little relevance to wild populations (Aubin et al. 1986; Curro et al. 1996). Thus it was useful to source wild growth rates from a similar population to estimate how long chicks from different size eggs would take to reach a safe weight.

Wild weight gain rates were measured in a North Island brown kiwi population at Lake Waikaremoana (central North Island, 430 km away) by McLennan (2004) over a 10 year period. This study site was broadly similar to mine, so their results should be applicable to my estimations. The Lake Waikaremoana site was located at 582 m elevation which was slightly higher than my Purua (387 m) and Rarewarewa (365 m) blocks. The vegetation at Lake Waikaremoana consisted mostly of old-growth mixed-beech and podocarp, with grassland and regenerating vegetation surrounding the shoreline. My study sites were generally broadleaf-podocarp forest, with some kiwi residing in exotic conifer woodlots, scattered native forest fragments in farmland, and hilly pasture. Mammalian predators were similar between both sites, particularly stoats, ferrets, and possums.

Weight gain rate in wild brown kiwi (n = 126) was described by the following second order polynomial equations (McLennan et al. 2004), for females (Equation 2) and males (Equation 3), where y = weight in grams and x = days of age since hatching.

$$y = -0.002x^2 + 4.613x + 294 \tag{2}$$

$$y = -0.002x^2 + 3.872x + 339 \tag{3}$$

The dataset I analysed did not record sex of chicks. McLennan (2004) mentioned that

growth rates were very similar between the sexes for the period that I was interested in (<800 g), and that differences in the growth curve equations reflect the higher weight adult females eventually reach. So I approximated a growth curve (Equation 4)(Figure 2.2) by averaging the equation coefficients of Equations 2 and 3. An assumption I have made here is that growth rate would be the same for different starting weights, however larger precocial chicks might forage more efficiently than smaller chicks and thus gain weight faster. This assumption could be resolved in the future by using better data which modelled the growth rates of individual chicks, and would likely improve the significance and magnitude of differences of these results.

$$y = -0.002x^2 + 4.243x + 317 \tag{4}$$

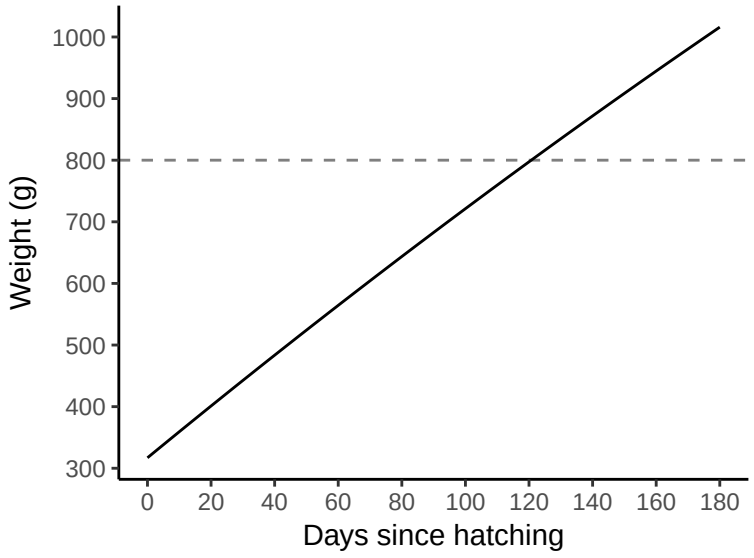

Figure 2.2: Relationship between weight and days since hatching in wild North Island brown kiwi. Dotted line is the safe weight of 800 g. Equation of line from McLennan et al. (2004).

2.2.4 Chick predation

As explained in the introduction, rate of chick predation in a wild, unmanaged North Island brown kiwi population varied according to weight (Table 2.1) (McLennan et al. 2004). Small chicks (<600 g) spent more time in the relative safety of the nest, so had a lower mortality rate than bigger chicks. Large chicks (601-700 g) were very active in

foraging trips away from the nest, but not yet large enough to defend against predators so suffered the highest mortality. Chicks between 701-800 g were also active but were of sufficient size to defend against small predators, so had the lowest mortality risk of juvenile kiwi. Once larger than 800g mortality risk was low for the rest of their lives and throughout adulthood (annual mortality 2.49%).

Table 2.1: Daily mortality rates of juvenile North Island brown kiwi in a wild population. Data from McLennan et al. (2004).

Weight class (g)	Daily mortality rate
<400	0.4
401-500	0.46
501-600	0.38
601-700	0.85
701-800	0.31

In order to estimate the probability of chicks of different hatch weights surviving to the safe weight of 800 g, I calculated the overall chance of survival according to the range of hatch weights in my study population. Survival rate to 800 g was calculated for various weight classes by incorporating exposure information (from the growth curve in Equation 4) with daily mortality risk (from Table 2.1) according to equation 5. Daily mortality risk was converted to daily survival probability by taking the inverse of the morality risk.

$$y = s^e \tag{5}$$

Where y = probability of survival in a given weight class, s = daily survival probability, e = exposure in days.

2.3 Results

2.3.1 Predicting chick weight

To assess the factors affecting chick hatch weight, I present model summary statistics of five models using various predictors (Table 2.2). This table allowed for the comparison of model suitability.

Table 2.2: Summary statistics for models predicting hatch weight of chicks. R^2 for lmer models includes both marginal, m, and conditional, c, statistics.

Model class	Chick hatch weight ~	F value	P value	DFs	R^2	AIC
`lm`	Fresh weight of egg	448.72	< 0.001	1, 109	0.80	910.9
`lm`	Day of the year	0.53	0.47	1, 109	0.00	1091.57
`lm`	Shape	9.52	0.003	1, 109	0.08	1082.81
`lmer`	Bill length	2.62	0.12	1, 29	$0.07m$, $0.70c$	945.03
`lmer`	Non-gravid weight	3	0.09	1, 28	$0.07m$, $0.69c$	951.38

Shape of egg ($\frac{Length}{width}$) initially appeared to be a significant ($p = 0.003$) predictor, however there were issues of multicollinearity between shape and fresh weight. Shape and fresh weight were significantly correlated (Pearson's r = -0.35, $p < 0.001$). When tested in a multiple regression (*chick weight ~ fresh weight + shape*), shape was no longer significant ($p = 0.401$) and fresh weight of egg remained significant ($p < 0.001$).

Here I present the multiple linear mixed effects model (Table 2.4) with additive explantory variables of fresh weight, day of year, shape, bill length, and non-gravid weight.

Table 2.4: Summary statistics for mixed effects model predicting the hatch weight of North Island brown kiwi chicks from Rarewarewa Reserve, Northland.

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	18.78	64.80	64.69	0.29	0.77
Fresh weight	0.79	0.05	75.21	16.83	< 0.001
Day of the year	0.00	0.02	93.56	0.20	0.84
Shape	4.37	29.69	76.60	0.15	0.88
Bill	-0.25	0.26	31.52	-0.96	0.35
Non-gravid weight	-0.01	0.01	31.49	-0.55	0.59

Clearly, looking at the significance of the explanatory variables, fresh weight is far more important in explaining the hatch weight of kiwi chicks than any of the other variables tested. When comparing the full model (Hatch weight ~ fresh weight + day of year + shape + bill + nongrwt) to the subset model (Hatch weight ~ fresh weight), R^2_M is higher in the subset model than the full model (0.8753 versus 0.8734). This indicates a slightly improved model fit in the subset model, and that the additional explantory variables are extraneous.

As expected, egg weight was strongly predictive of chick size (Figure 2.3) and no other tested variable had an effect on chick weight. Equation 6, which included fresh egg weight, was the best model according to both R^2 and AIC.

$$c = -11 + 0.77 * e \tag{6}$$

Where c = hatch weight of chick (g), e = fresh weight of egg (g).

Hatch weight of chicks in my dataset ranged from 254-431 g, mean = 345 ± 6.09 g (± 95% CI). Fresh weight of eggs ranged from 336-551 g, mean = 462 ± 7.1 g (± 95% CI).

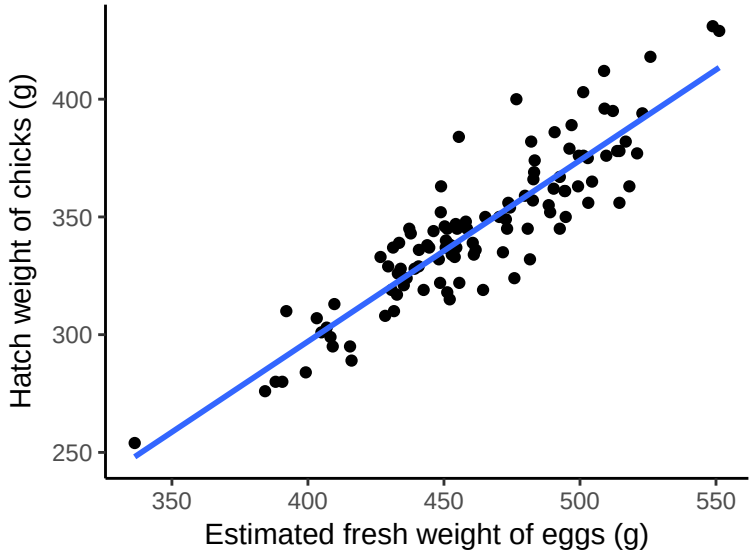

Figure 2.3: Relationship between estimated fresh weight of eggs and the hatch weight of eggs in a North Island brown kiwi from Rarewarewa Reserve, Northland, New Zealand.

Model fit was not improved by log transforming either of these variables. Linear model assumption tests (homoscedasticity of residuals, normality of residuals, and etc.) were acceptable. Increase in residual scatter with increase in egg weight was non-significant (Shapiro-Wilk normality test of residuals: $p = 0.182$).

2.3.2 Relationship between chick size and fitness

To estimate the importance of hatch weight of chicks on lifetime fitness, I estimated the number of days spent under 800 g and compared the larger and smaller chicks in our data (Table 2.5). The growth curve under 800 g (Figure 2.2) was nearly linear, with the slope indicating that chicks put on 3.94 grams per day. The largest chicks present in our population took around 93 days to reach safe weight, the smallest took 137 days. Average sized chicks would take around 114 days to reach this same weight. Note that the repetition of the number of days it takes to get through a 100 g weight class (25 days) was due to these growth rates being estimated from Equation 4.

Table 2.5: Estimated exposure of wild North Island brown kiwi chicks of different starting weights in each weight class.

Size class	Weight (g)	Days <400 g	Days 401-500 g	Days 501-600 g	Days 601-700 g	Days 701-800 g	Total days <800 g
Max	431	0	18	25	25	25	93
Upper quartile	363	9	25	25	25	25	109
Median	345	14	25	25	25	25	114
Lower quartile	327	19	25	25	25	25	119
Min	254	37	25	25	25	25	137

Predation risk under 800 g varied according to weight (Table 2.1). Number of days under 800 g was a simple metric of time spent at risk but it did not quantify predation risk. Here I present the estimated predation risk for chicks with different starting weights in accordance with their exposure in each weight class (Table 2.7).

Table 2.7: Estimated probability of survival of wild North Island brown kiwi chicks through different weight classes and to 800g according to exposure and daily mortality risk.

Size class	Survival < 400 g	Survival 401-500 g	Survival 501-600 g	Survival 601-700 g	Survival 701-800 g	Total survival to 800 g
Max	1	0.92	0.91	0.81	0.93	0.63
Upper quartile	0.85	0.89	0.91	0.81	0.93	0.52
Median	0.84	0.89	0.91	0.81	0.93	0.51
Lower quartile	0.82	0.89	0.91	0.81	0.93	0.5
Min	0.75	0.89	0.91	0.81	0.93	0.46

Small kiwi chicks had a lower probability of reaching the safe weight of 800 g than larger chicks, due to the extra risk early in their life.

2.4 Discussion

The weight of freshly laid brown kiwi eggs (which can be estimated using the dimensions of an egg of any age) was a good predictor of the weight of chicks at hatching. Day of the year might have been expected to be a useful predictor because there is strong seasonal distribution of egg laying; however this did not turn out to be important for predicting chick size. The length of the female parent's bill and non-gravid body weight might also reasonably have affected chick weight as these are measures of body size in kiwi. This could occur either through producing larger eggs (Chapter 4 of this thesis) or through producing higher quality egg contents irrespective of physical size (Ahn et al. 1997; Finkler et al. 1998). However, when both of these explanatory factors are properly accounted for using a generalised linear mixed model it is apparent that the explanatory power comes solely from egg weight.

The fresh weight of a chick had a large effect on the number of days that it spends at risk

under 800g. The growth rate was approximately linear during this juvenile development period, indicating that larger chicks do not grow at a faster rate than smaller chicks. Instead the reduction in number of days at risk occurred simply because a larger-born chick had less weight to put on to reach a safe weight than smaller-born chicks. The large chicks in our data took 44 days less to reach 800 g (Table 2.5) compared to small chicks. The estimated mortality risk of reaching 800 g for large chicks was 37% compared to 54% of small chicks (Table 2.1). This decreased chance of mortality is because larger chicks spend less time in the riskier smaller weight classes. The largest chicks in our study would have spent no time at all in the smallest weight class (which had a moderate daily risk of mortality) and spent a reduced amount of time in the next weight class (which had the highest daily risk of mortality). As current predation rates of young kiwi are *c.* 50% per annum and would only need to drop to approximately 33% per annum for populations to stabilise (McLennan et al. 1996), this highlights the significance of these chick weight differences because large chicks would lead to population stabilisation and small chicks would lead to population decline.

McLennan (2004) suggests that slow juvenile growth is the primary reason why brown kiwi populations decline in the presence of unmanaged stoat populations. They also give an example that if kiwi grew at the same rate as megapods (Megapodiidae - family of superprecocial browsers including brush-turkeys and scrubfowl), kiwi would reach the safe weight of 800 g 66 days quicker. Based on population modelling this reduction in exposure would decrease predation losses from 61% to 31%, allowing populations to stabilise. Although this comparison between the growth rate of kiwi and megapods is just hypothetical, it does provide a useful framework for assessing the magnitude of survival and exposure differences we see in our study population, as I have just demonstrated.

Inherent differences between the growth rates of different populations are certain to exist to some degree, but the significance of these differences has not been fully investigated. Differences in growth rates of chicks in Trounson Kauri Park residing in different habitat types was suggested to result from different levels of resource availability (Gibbs & Clout 2003). It was also suggested that large differences between growth rates in Trounson and Lake Waikaremoana populations were due to soil type; and thus food availability. However, Gibbs and Clout (2003) mention that subsequent examination and unpublished data may diminish any significant differences between these geographically isolated populations, such that further investigation would be required.

3 Assortative mating: who chooses who?

3.1 Introduction

Assortative mating, particularly for body weight, is one of the most commonly observed mating patterns in animals (Crespi 1989). Relevant avian characters could include age, body size, or plumage colouration (MacDougall & Montgomerie 2003; Helfenstein et al. 2004). The evolution of assortative mating may be explained by three hypotheses (Crespi 1989): (1) mate choice, where the choosy sex selects particular characters because they will benefit reproductively, (2) mate availability, where individuals with particular characters are simultaneously available for mating, (3) mating constraints, where particular characters excludes some pairings due to difficulties in courtship, pairing, or mating. Little conclusive evidence of assortative mating has been found for reversed size dimorphism (female larger than male) bird species (Mueller 1992; Warkentin & James 1992). It has been suggested that if assortative mating were to occur in reversed size dimorphism species, it would be in the *negative* direction (dissimilar pairings) (Olsen & Olsen 1987; Sandercock 1998). North Island brown kiwi exhibit reversed size dimorphism, with females weighing 35% more than males (Heather et al. 2000) and having 30% longer bill lengths (Cunningham & Castro 2011). I could not find any studies that have tested assortative mating in kiwi.

Kiwi *Apteryx* mostly have long-term partnerships and very high partner fidelity (Taborsky & Taborsky 1999). Kiwi divorce is thought to be "forced" upon the pair by highly female-biased sex ratios (which may result because of reduced predation on the larger female sex) and does not confer any reproductive advantage (Taborsky & Taborsky 1999). North Island brown kiwi in Northland forests have been observed to be generally monogamous, even in populations with female-biased sex ratios (Taborsky & Taborsky 1991). In male-biased populations, surplus unpaired males maintained territories twice the size of pair males' territories, but did not take part in reproduction (Taborsky & Taborsky 1991).

In this Chapter I aim to firstly assess the sexual dimorphism in North Island brown kiwi for five measures of body size (bill length, body weight, tarsus width, tarsus depth, tarsus length). Then I will assess, for characters showing sexual dimorphism, the extent of assortative mating in paired kiwi.

3.2 Methods

3.2.1 Morphological size characters

I have selected five characters (weight, bill length, tarsus width, tarsus depth, tarsus length) for comparison of body size between sexes. Body weight would vary for an individual depending on food availability, time since breeding, etc. I only used weights for females recorded when they were non-gravid so that the weight of eggs would not be included. Bill length is static in kiwi after reaching adulthood so provides a highly repeatable measure, and is also related to maximum depth of feeding (which has potential consequences for inter-sexual niche differentiation). Tarsus measures had a low degree of repeatability between different observers, owing to the difficulty in taking these field measures. For each of the five morphological size characters, multiple measurements (n = 1-48) were taken over an individual's lifetime depending on how many times they were encountered, so I have used the mean of these measurements.

3.2.2 Extent of sexual dimorphism

To quantify the extent of sexual dimorphism I performed two-sample t-Tests using the R `stats` package. The morphological character of interest was set as the vector to compare, and sex was used as the partitioning variable.

Overlap between the male and female distributions was quantified according to the overlapping coefficient (OVL) as described by Inman (1989), using the `OVL` function in the `LPS R` package. OVL is simply a measure of agreement between two probability distributions, and is measured as a proportion from 0 (complete disagreement) - 1 (complete agreement).

3.2.3 Pairings

In order to determine pairings of kiwi I utilised my 496-egg dataset which contained the identity of both male and female parents for each egg record. These parent pairs were cross-tabulated and a table of counts of all parent combinations was produced. Kiwi are generally monogamous (see above), but 17% of the pairings were found to be extra-pairings. These extra-pairings generally only produced one nest (1-2 eggs), and

the field methodology could not determine with absolute certainty the identification of the parents, thus I restricted the parent combination cross-tabulation to only include the pairings that produced the greatest number of eggs where a bird had several different pairings. This reduced the total number of pairings from 110 to 91.

3.2.4 Assortative mating relationship

To test the significance of relationship between the different sexes in a kiwi pair, a linear model was fitted using the male measure as the response variable and the female measure as the explanatory variable. The explanatory factor was selected to be the female measure because it is assumed that females are the choosy sex in reversed size dimorphism species (Catry et al. 1999). Fit of the models were tested for linear model assumptions (such as normality of residuals) using the base `R` package `stats`. No transformations were needed to meet these assumptions.

3.3 Results

3.3.1 Sexual dimorphism in brown kiwi

Across all my five chosen measures of size, males were consistently smaller than females (Figure 3.1). Differences between sexes were most pronounced for bill length and weight. There was greater overlap between sexes, as measured by overlapping coefficient (OVL), in the three tarsus measurements: width (23.74%), depth (18.71%), and length (14.94%) than for bill length (0.63%) or weight (11.29%). Differences of all the characters were highly significant (Table 3.1).

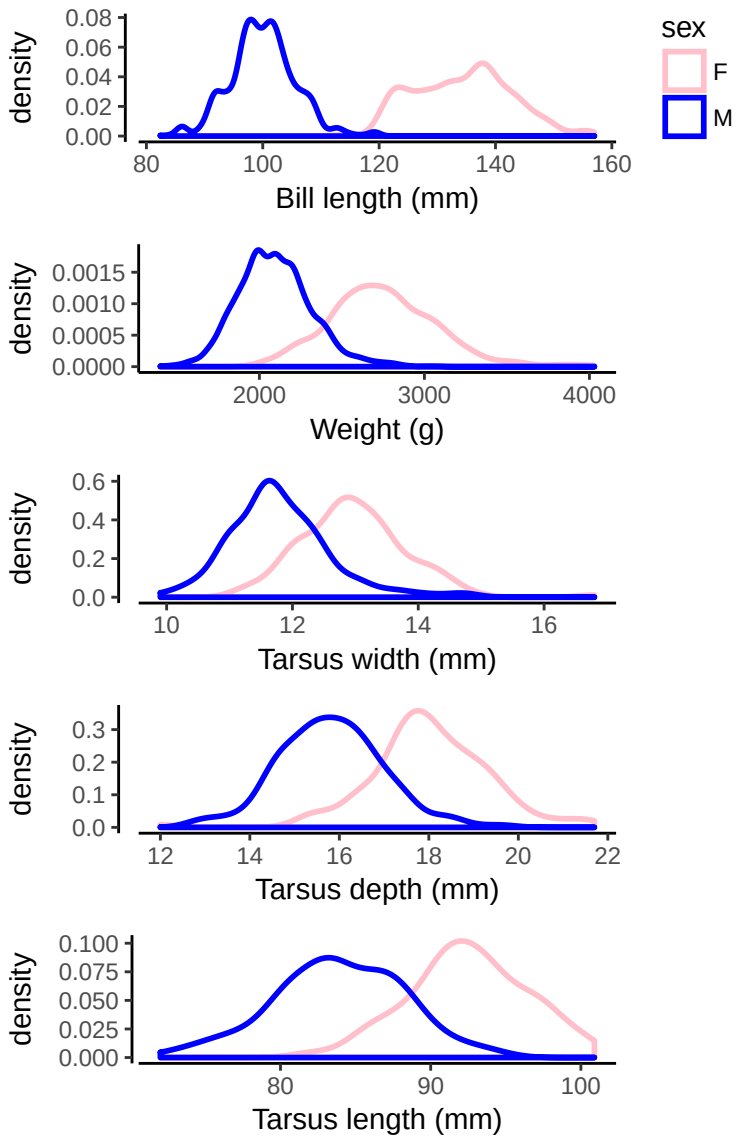

Figure 3.1: Distribution of five size variables for North Island brown kiwi males and females from Rarewarewa Reserve, Northland.

Table 3.1: Measurements of North Island brown kiwi from Rarewarewa Reserve, Northland. Mean ± standard error of mean (n). Student's t-Test of difference between sexes.

Variable	Males	Females	t	P
Bill length (mm)	100.02 ± 5.54 (219)	134.43 ± 8.3 (210)	116.09	< 0.001
Weight (g)	2093.48 ± 223.07 (221)	2749.42 ± 325.07 (210)	60.04	< 0.001
Tarsus width (mm)	11.79 ± 0.8 (110)	12.97 ± 0.84 (110)	12.18	< 0.001
Tarsus depth (mm)	15.81 ± 1.16 (110)	18.03 ± 1.34 (110)	15.02	< 0.001
Tarsus length (mm)	83.88 ± 4.35 (109)	92.5 ± 3.96 (110)	17.73	< 0.001

3.3.2 Kiwi-pair body size relationships

There was no detectable assortative mating for bill length in either direction (Figure 3.2). Any trend present was non-significant ($R^2 = 0.002$, df = 87, p = 0.644).

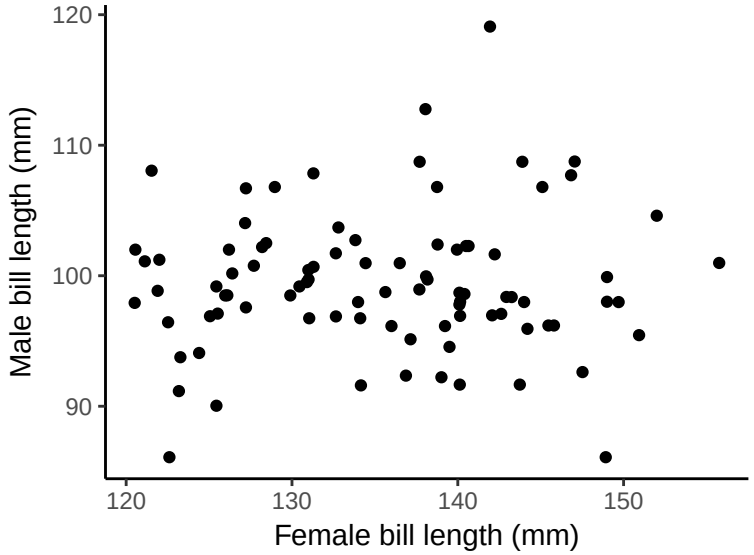

Figure 3.2: Comparison of bill length between male and female North Island brown kiwi breeding pairs from a population in the Rarewarewa Reserve near Northland, New Zealand.

There was also no assortative mating in weight in either direction (Figure 3.3), as a non-significant trend was detected ($R^2 = 0.001$, df = 87, p = 0.736).

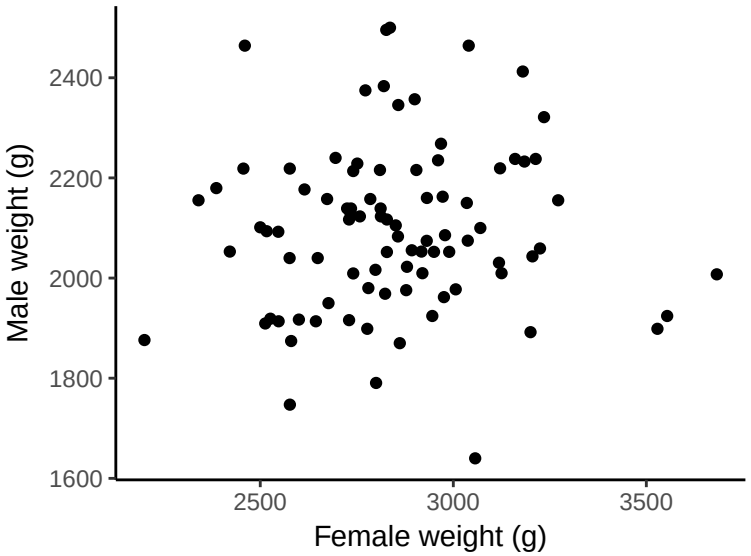

Figure 3.3: Comparison of body weight between male and female North Island brown kiwi breeding pairs from a population in the Rarewarewa Reserve near Northland, New Zealand.

The three tarsus measurements also showed non-significant assortative mating (Figure 3.4): tarsus width ($R^2 = 0.011$, df = 70, p = 0.39,), tarsus depth ($R^2 = 0.013$, df = 70, p = 0.334), or tarsus length ($R^2 = 0.043$, df = 70, p = 0.083).

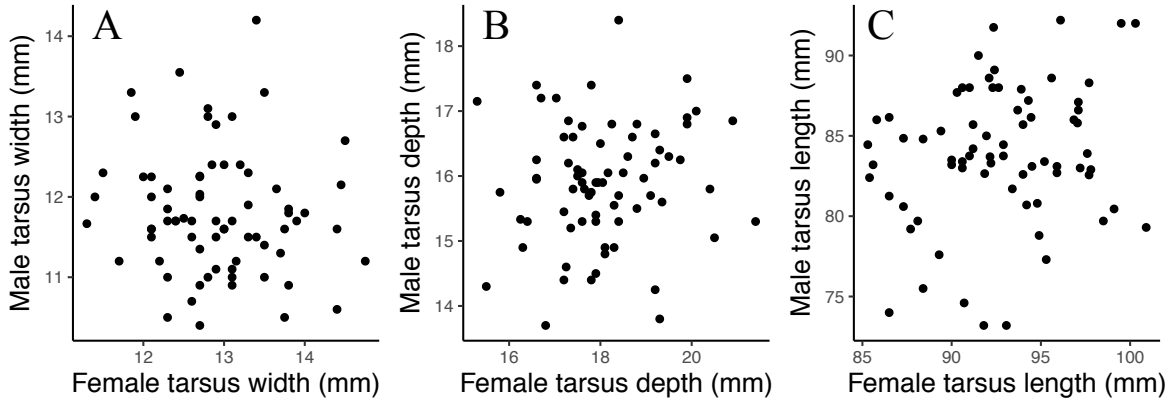

Figure 3.4: Comparison of tarsus width (A), depth (B), and length (C) between male and female North Island brown kiwi breeding pairs from a population in the Rarewarewa Reserve near Northland, New Zealand.

3.4 Discussion

I found no evidence of assortative mating in any of the morphological characters that I have tested. There are other metrics which would be interesting to test, but that I did not have data for (such as age or fecundity).

Bill length was the character for which I most expected to find evidence of assortative mating, as it had the greatest sexual dimorphism. Mueller (1985) predicted that if the differentiation of foraging niches had been important in the evolution of reversed size dimorphism, the dimorphism of trophic structures (appendages used directly in foraging) would be greater than the dimorphism in body size or appendages not directly used in foraging. Bill length in kiwi could certainly be regarded as a trophic structure, as it is directly used for foraging underground or underwater (Reid et al. 1982). In a North Island brown kiwi population on Ponui Island it was found that females with their longer bills could probe in soil on average 30% deeper than males (Cunningham & Castro 2011). It has also been reported that during incubation females remained in the vicinity of the nest and shared the same foraging grounds as their male partners, even feeding together when the male left the egg alone at night (Colbourne 2002).

Applying Mueller's (1985) foraging hypothesis: niche differentiation may have been expected to be the important driving force for the evolution of reversed size dimorphism in brown kiwi, and thus kiwi might also assortatively mate across bill length for the same reason. However, I found no evidence of this for this population of North Island brown kiwi. Perhaps this hypothesis does not apply to brown kiwi or perhaps other selective pressures for males to be large (e.g. because they are solely responsible for incubation, or due to extensive mate-guarding (Taborsky & Taborsky 1999)) diminishes any significant effect.

It was also surprising that brown kiwi did not appear to assortatively mate for weight, as there was a large amount of sexual dimorphism. A few other studies have found evidence of assortative mating based on weight (Bowman 1987), but these same studies also mention the difficulty in finding datasets that have reliable measures of weight (which aren't affected by seasonality or breeding status). In my dataset, the weights for an individual are averaged from multiple measurements over their lifetime. It is possible that these weights do not accurately represent the weight at time of breeding or pair-choice, but on the other hand, these averaged measures provide a better long

term picture of an individual's size without short term fluctuations due to seasonality or recent breeding status.

It was not surprising that I could not find evidence of assortative mating for the three tarsus measurements, as these had the least sexual dimorphism and are probably only weakly associated with body size and are not foraging appendages in kiwi. Unlike raptors or owls which use their feet for grabbing prey (Mueller 1986), kiwi do not use their feet directly for feeding so these could not be considered a trophic structure (Muller's foraging hypothesis did not apply).

Unfortunately these results provide inconclusive evidence of whether North Island brown kiwi truly do (or would, given more natural conditions) assortatively mate. Reverse sexual dimorphism was certainly present in a number of morphological characters, and trophic structures showed greater sexual dimorphism than non-trophic structures, so the mechanisms and theory was in place to support that assortatively mating was likely - but I could not find any evidence of this. So if it seems more likely that North Island brown kiwi should assortatively mate than not, why was any trend in this population non-significant? This was a mainland kiwi population, and whilst various predator management programs were in place, the density of kiwi was presumably lower than would have been in the pre-human Northland forests. With lower kiwi densities, the opportunity for mate choice is diminished (as there are less other kiwi encountered to choose from), so kiwi may be choosing less desirable or less optimal partners. Why would kiwi choose to enter less optimal pairings, especially considering they are monogamous with long-term pair bonds? The negative effect to lifetime fitness of potentially missing out on reproductive opportunities by being fussy about mate choice must be greater than the positive effect of assortatively mating (which has been shown in fish by Taborsky et al. (2009)). The question as to whether kiwi assortatively mate therefore may be better served by data originating from populations with high kiwi densities (lots of mate choice), and more natural conditions (same selective pressures as during their evolutionary history). I suggest repeating the methodology of this Chapter using data from kiwi populations from offshore islands (e.g. Kapiti Island, Little Barrier Island, Motuara Island) or mainland reserves (e.g. Zealandia, Maungatautari). Of course, it is entirely possible that kiwi do not assortatively mate, and never did, but at least the results of this Chapter do not provide solid evidence of this.

4 Predictors of egg size: what factors are associated with large eggs?

4.1 Introduction

A large amount of variation in the size of eggs (50-200% within a species) has been reported for many avian species (reviewed by Christians (2002)). But why is this so? Why do parents not usually produce eggs close to some optimal size? To answer this we then need to ask; how large should this optimal egg size be for a given species, or more precisely: what factors determine how much parents should invest in each of their offspring in order to gain maximum fitness? Of course, variation is inherent in biological systems, so examining egg size variation only becomes interesting if the variation is large enough that certain individuals appear to be maladapted to their environment (because natural selection would tend to decrease the frequency of such phenotypes).

Well-provisioned offspring tend to survive better (see Chapter 2), but investing in offspring costs parents. It can cost parents in terms of their own immediate survival (Monaghan et al. 1998) (thus completely eliminating future offspring), or it might cost them in how much they can invest in future offspring (Plaistow et al. 2007) (thus reducing future offspring). The product of clutch size and egg size determines the total energetic investment provided by parents to their offspring (Flint & Sedinger 1992), so there is a trade-off between number of offspring and investment given to each of the offspring (Smith & Fretwell 1974; McGinley et al. 1987). The different sides of this trade-off balance affect parental fitness through different mechanisms; investment in offspring is positively correlated with initial size and survival for chicks (see Chapter 2), whereas clutch size affects chick survival via the potential number of offspring produced (Lessells 1986).

It is difficult to determine optimal egg size for a given species due to the complex interactions an animal has with its environment (Parker & Begon 1986), and due to spatial and temporal variation. The factors that cause variation in egg size, and the consequences remain unclear (Christians 2002). A review by Christians (2002) suggests that a significant proportion of variation (~70%) in egg size is due to between-female variation, but the traits of females that influence egg size are unclear. Female mass or size rarely explains more than 20% of the variation in egg size of avian species, but in

non-avian species (fish and turtles) female mass or size commonly explains a greater proportion of the variation in egg size (Christians 2002). As mentioned in Chapter 1, clutch size appears to covary with egg size in many species, generally decreasing egg size with increasing clutch size (Williams 2001). Intra-clutch egg size variation is sometimes proposed as adaptive (Slagsvold et al. 1984; Williams et al. 1993), or a constraint (Arnold 1991; Nilsson & Svensson 1993; Kilpi et al. 1996) or both (Vinuela 1997; Aparicio 1999), but no clear consensus exists.

Kiwi have many unusual reproductive and physiological traits, and in some ways have more in common with mammals than other birds (Reid & Williams 1975; Calder 1978; Baker et al. 1995). Particularly relevant to this chapter is their slow growth (See Chapter 1 for further details) and large eggs, which are both explained by their evolutionary history and life history. Life-history theory predicts that animals should grow as fast as possible (within physiological constraints), why then do kiwi grow so slowly? It is a general pattern of oceanic island animals to reduce energy use, often through adaptations such as flightlessness (McNab 1994). McLennan et al. (2004) suggests that the slow growth of kiwi was driven mainly by energetic considerations rather than predator avoidance. Fast growth is energetically demanding, and kiwi have been able to get away with slow development due to low predation rates. New Zealand, like many other oceanic islands, does not naturally have mammalian predators. What avian predators New Zealand has, or did have, kiwi largely avoided by being nocturnal (Le Duc et al. 2015), cryptically-coloured and cryptically-behaved. The landscape of New Zealand was dominated by low productivity, infertile, long-lived vegetation types for thousands of years during the Oligocene (Cooper 1995) so energetic considerations were important for kiwi. Kiwi responded by developing a whole package of unusual traits: flightlessness, low metabolic rate, small clutch size, slow juvenile development, extreme precociality and large eggs. It really is a whole package too, because many of these traits are interdependent.

In this chapter I aim to:

1. Describe the amount of variance in the fresh egg weight of North Island brown kiwi from my study population in Rarewarewa Reserve, Northland, New Zealand.
2. Determine if females vary in the mean fresh weight of eggs they produce.
3. Determine what factors influence fresh egg weight in North Island brown kiwi, specifically;
    - female body size and weight
    - male body size and weight
    - phenological metrics: clutch size, sequence of nest in year, sequence of egg in year, and sequence of egg in nest
    - effect of other covariates: site, and year

4.2 Methods

4.2.1 Estimating fresh weight of eggs as response variable

See Chapter 2 methods for full details of how I estimated fresh weight of eggs. Briefly, I used an equation (Equation 7) from Hoyt (1979) to estimate the fresh weight of eggs (W) using length (L), breadth (B) and a density coefficient (K_w). I used a K_w value of 0.5616 (g/mm^2) $\pm$ 0.0087.

$$W = K_w L B^2 \tag{7}$$

4.2.2 Statistical analysis

4.2.2.1 Repeatability

Repeatability is a measure of the proportion of variance in a character that occurs among rather than within individuals. I tested repeatability of estimated fresh egg weight amongst individual females, using the `rptR` package. Fresh egg weight was a Gaussian response distribution, so I used the `rptGaussian` function which calculated point estimates, 95% CI of the estimate, and performed significance testing of repeatability. The setup of this model was similar to my other linear mixed models (infact `rptR` calls upon `lme4` S3 model objects), where the response variable was estimated fresh

egg weight and the only explanatory variable was a random term for female identity, fitted using the restricted maximum likelihood (REML) procedure. 1000 parametric bootstrap samples were used for interval estimation and significance testing.

Repeatability was calculated according to the following equation, where σ_α^2 is the between-group variance and σ_ϵ^2 is the within-group variance.

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\epsilon^2} \tag{8}$$

4.2.2.2 Model selection

To test which factors were useful in explaining the variation in estimated fresh egg weight, I utilised the Information Theoretic Model Comparison (ITMC) approach to model selection as described by Burnham and Anderson (2002). This approach is an alternative to the usual selection of a single "best" model via a particular criterion, and instead favours multimodel inference (formal statistical inference from all plausible models in a set). I used generalised linear mixed models (GLMMs) because mixed models allow for both fixed and random effects. A single random term for female identity was employed to take into account the structure of the dataset (females laid multiple eggs within and between years, so data points were not all independent of each other). It was sufficient to use a single random term just for female identity and not also for male identity because the pairings of individuals was almost always monogamous (a formal test of the importance of a second random term for male identity confirmed no added benefit of a second random term for male identity). A global model was set using *a priori* hypotheses of important explanatory factors (Table 4.1) to test against other candidate subset models.

Table 4.1: Reasons for including each explanatory factor in the global model

Explanatory factor	Hypothesis	Reference
Female body weight	Larger females well provisioned to meet energetic demands of producing large eggs	(Rahn et al. 1975)
Female bill length	Structurally large females could produce larger eggs	(Congdon & Gibbons 1985)
Male body weight	Well provisioned birds can incubate for longer (larger eggs need longer incubation) so may favour differential allocation by females	(Hanssen et al. 2002)
Male bill length	Possible differential allocation by females	(Bolund et al. 2009)
Site	Differing resource availability	(Gibbs & Clout 2003)
Start laying date	Strong seasonality in kiwi egg laying	(Cockrem et al. 1992)
Clutch size	Larger clutches costly to produce	(Erikstad et al. 1993)
Year	Differing resource availability	(Gibbs & Clout 2003)
# nest in year	Reduced egg size may be associated with costly egg production	(Monaghan & Nager 1997)
# egg in year	Reduced egg size may be associated with costly egg production	(Monaghan & Nager 1997)
# egg in nest	Strategic allocation ("last chick disadvantage")	(Pierotti & Bellrose 1986)

This global model was assessed for goodness-of-fit, because if the global model was not a well fitting model then I would merely be selecting the best of a set of poor-fitting models. Outliers, high leverage points, and residuals were examined using standard tests and were acceptable for model assumptions.

Candidate models included all possible combinations of the global model's explanatory variables. Model selection based on Akaike's Information Criteria ($AICc$) was conducted on the full set of candidate models. $AICc$ was chosen because it has an additional bias-correction term for second-order correction compared to AIC, necessary if the ratio of n/K is small (n = sample size, K = number of parameters). If n/K is large then $AICc$ and AIC perform similarly. The use of AICc requires that relative comparisons be made on the same dataset, therefore any observations in the dataset with missing values for any of the parameters in the global model were removed.

To select candidate models, $AICc$ and log-likelihood values values were estimated using the `lme4` package for each model in the set and then ranked by $AICc$. The most parsimonious model was the one that had the lowest $AICc$ value, and Δ values (Δ_i = $AICc$ - $AICc_{min}$) for subsequent models was calculated using the `MuMIn` package. Models for which $\Delta_{\mathrm{i}} \geq 2$ are considered to have substantial support (Burnham & Anderson 2002).

To compare models, Akaike weights (ω_i) were scaled so that values for all models summed to 1. Akaike weights provide an approximate probability of model i being the best model and are a useful metric for comparing the relative strength of each model.

Models with $\Delta AICc > 1$ were selected and presented in the results section (n = 6). Using this strict criterion was neccessary because of the large number of models (n = 18) selected under the $\Delta AICc > 2$ criteria.

Model goodness-of-fit was assessed using a modified version of the coefficient of determination R^2 for GLMMs, as described by Nakagawa (2013). Marginal (R^2_m) and conditional (R^2_c) coefficient of determination values were calculated using the `MuMIn` package.

4.2.2.3 Model averaging

Prediction of fresh egg weight was an aim of this chapter. In linear-regression based variable selection such as this, it is proposed that choosing a single "best" model would be unwise because that "best" model would often be highly variable (i.e. that best model would vary from dataset to dataset, even if replicate datasets were collected under the same underlying mechanisms) (Burnham & Anderson 2002). Model averaging provides stabilised model inference as inference is instead related to a number of models

(which reduces model selection bias).

In the previous section I described how a set of models was selected, but as no single model stood out clearly as being the best (i.e. $\omega > 0.90$), it was useful to use model averaging to predict fresh egg weight values. Model averaged estimates $\bar{\theta}$ of each parameter θ were generated using the `model.avg` function in the `MuMIN` package (full details can be found in Burnham & Anderson (2002)). Estimates of each model parameter were weighted by their Akaike weights, ω_i, according to Equation 9.

$$\bar{\theta} = \sum_{i=1}^{R} \omega_i \hat{\theta}_i \tag{9}$$

4.3 Results

4.3.1 Observed egg size variation

Mean egg size was 124 x 79.8 mm (n = 496). Mean estimated fresh egg weight was 445 ± 45 g (± SD), range = 317-551 g (Figure 4.1). Repeatability of estimated fresh egg weight by females was high (R = 0.67 ± 0.06 95% CI, $p < 0.001$).

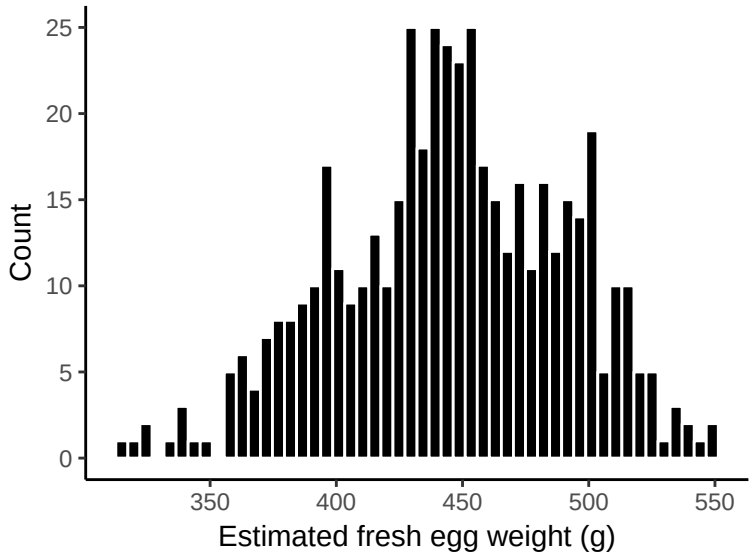

Figure 4.1: Variation in the estimated fresh egg weight of 496 North Island brown kiwi eggs from Rarewarewa Reserve, Northland, New Zealand.

4.3.2 Factors that explain variation in estimated fresh egg weight

From the global model, the entire set of candidate models was ranked by $AICc$. $\Delta AICc$ was calculated from the baseline of $AICc_{min}$. Here I present the top models with $\Delta AICc > 1$ (Table 4.3).

Table 4.3: Selected set of candidate models ($\Delta AICc \geq 1$) order by $AICc$. Model variable codes: 1 = Male bill length, 2 = Male body weight, 3 = Clutch size, 4 = Female body weight, 5 = Site, 6 = Sequence of eggs in a year.

Model	*df*	*logLik*	*AICc*	$\Delta AICc$	ω	R^2_m	R^2_c
245	8.00	-1347.69	2711.90	0.00	0.20	0.312	0.763
2345	9.00	-1346.70	2712.05	0.15	0.19	0.312	0.767
1245	9.00	-1346.75	2712.14	0.24	0.18	0.320	0.769
12345	10.00	-1345.70	2712.20	0.30	0.17	0.320	0.772
2456	9.00	-1347.04	2712.72	0.82	0.13	0.309	0.767
23456	10.00	-1346.00	2712.79	0.89	0.13	0.309	0.771

This summary table indicates that male bill length, male body weight, female body weight, clutch size, site, and sequence of eggs in a year are all important predictors in a number of models which do a good job of predicting fresh egg weight. As no ω is large (i.e. ≥ 0.90), no particular model stands out as clearly being the best and as such all of these models should be considered useful.

In these top performing candidate models male body weight, female body weight and site appear in every model (Table 4.4). Clutch size, male bill length and sequence of egg in a year appear in a subset of these models. The relative importance of the different variables (Table 4.4) also confirms that male body weight, female body weight and site are very important predictors of estimated fresh egg weight.

Table 4.4: Assessment of the relative importance of individual model variables based on Akaike weights and number of times a variable appears in the selected set of candidate models.

Variable	Importance	*N*
Male weight	1.00	6
Female weight	1.00	6
Site	1.00	6
Clutch size	0.49	3
Male bill length	0.35	2
# egg in year	0.26	2

Because no particular model stood out as being a single "best" model, each of the set of candidate models were used to contribute to one averaged model (Table 4.5).

Table 4.5: Model summary statistics for averaged model predicting fresh egg weight of North Island brown kiwi.

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	196.28	70.47	70.74	2.77	0.01
Male weight	0.05	0.02	0.02	2.80	0.01
Female weight	0.06	0.02	0.02	3.59	0.00
SiteP	15.93	10.53	10.58	1.51	0.13
SiteRp	31.24	16.08	16.15	1.93	0.05
SiteRr	-20.48	9.47	9.52	2.15	0.03
Clutch size * 1000	-0.01	0.01	0.01	0.70	0.48
Male bill length	-0.21	0.38	0.38	0.55	0.58
Sequence of egg	0.43	1.02	1.02	0.42	0.67

Using this averaged model I predicted fitted values for all the main effects (Figure 4.2), to explore the effect that each factor had in explaining estimated fresh egg weight. This, combined with Table 4.5, indicated the strength and direction of each of these main effects. It was evident that increased body weight of both sexes of parent had a large positive association with estimated fresh egg weight (Figure 4.2A & B). Increasing clutch size decreased the fitted values of fresh egg weight (Figure 4.2C), which was the opposite of the effect if simply looking at the raw data without the benefit of the mixed

effects model (Figure 4.3). The effects of male bill length and sequence of egg were weak, but male bill length had a small negative association (Figure 4.2D) and sequence of egg had a very small positive association (Figure 4.2E). There were differences in average estimated fresh egg weight between sites (Figure 4.2F), with the largest eggs being found at Riponui (Rp) followed by Purua (P), Hodge's Bush (H), and Rarewarewa (Rr) respectively.

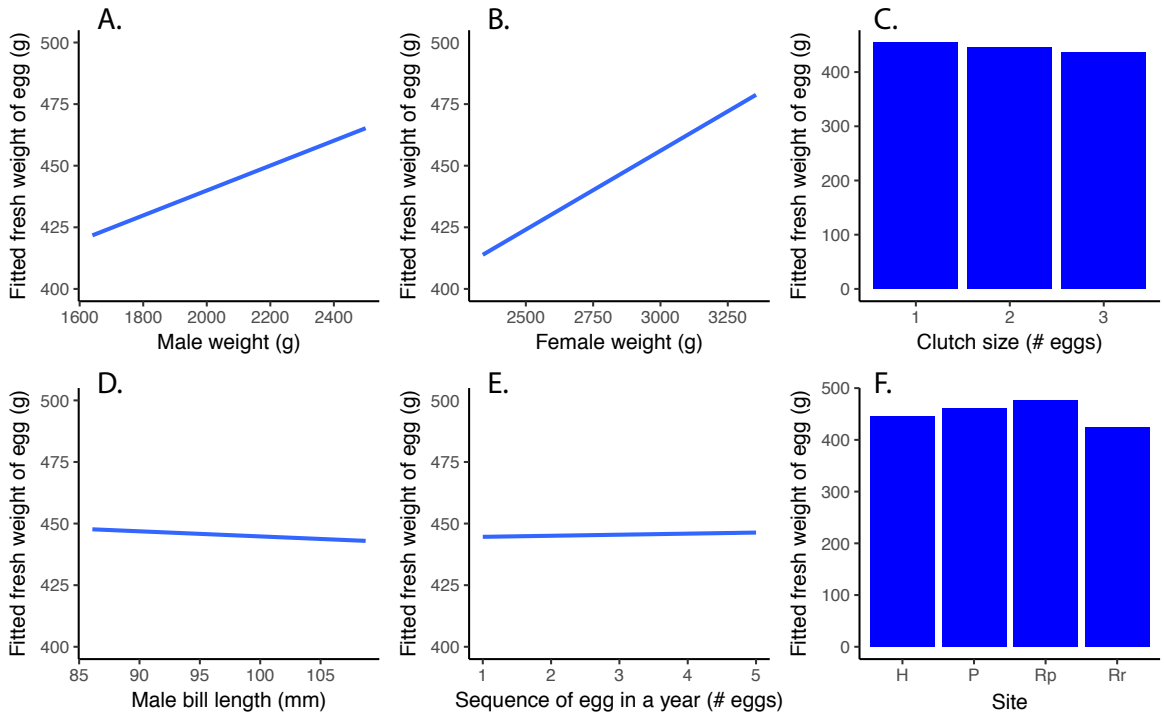

Figure 4.2: Fitted values for the model averaged main effects for (A.) male body weight, (B.) female body weight, (C.) Clutch size, (D.) male bill length, (E.) Sequence of egg in year, (F.) Site: Riponui *Rp*, Purua *P*, Hodge's Bush *H*, and Rarewarewa *Rr*.

If just looking at a simple plot of clutch size versus fresh egg weight (Figure 4.3) it might appear that estimated fresh egg weight increases with increasing clutch size. However two issues with this approach are that it does not take into account the nested structure of my data, nor does it take into account other covariates which may explain this variation. In other words, in the simple analysis, females that chose to lay larger clutches also laid larger eggs per clutch. These were probably higher quality birds in higher quality sites than the females that chose to lay 1-egg clutches. Once that effect was controlled for, there was a modest decrease in egg size with larger clutches (from

455 g in 1-egg clutches to 436 g in 3-egg clutches).

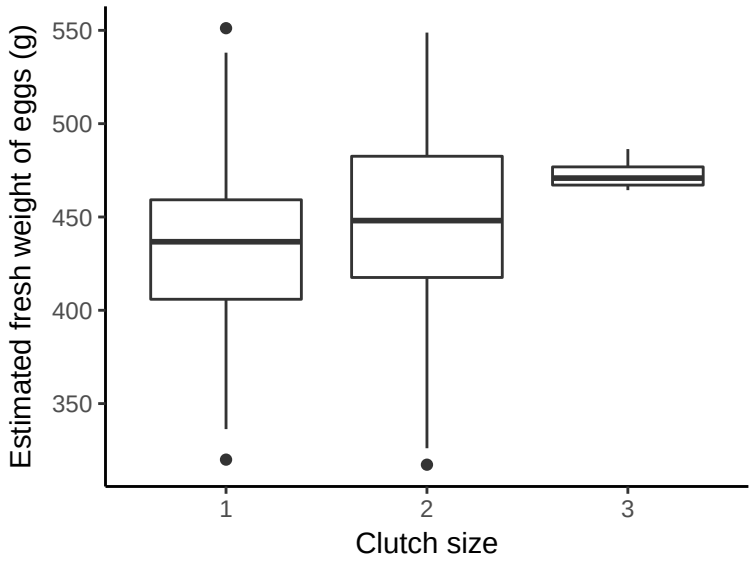

Figure 4.3: Simple analysis of clutch size versus estimated fresh weight of eggs in North Island brown kiwi, which does not take into account special data structure or other covariates. Note that 3-egg clutch eggs were rare in these data (n = 4 versus 85 and 483 for 1- and 2-egg clutches respectively).

4.4 Discussion

The estimated fresh egg weights were approximately normally distributed, with a single peak around the mean of 445 g. The range in fresh egg weights (234 g) is thought to have significant fitness consequences (see Chapter 2). The ratio of the largest egg weight in the population to the smallest was 1.74, which was at the high end relative to 39 other avian species (Figure 4.4).

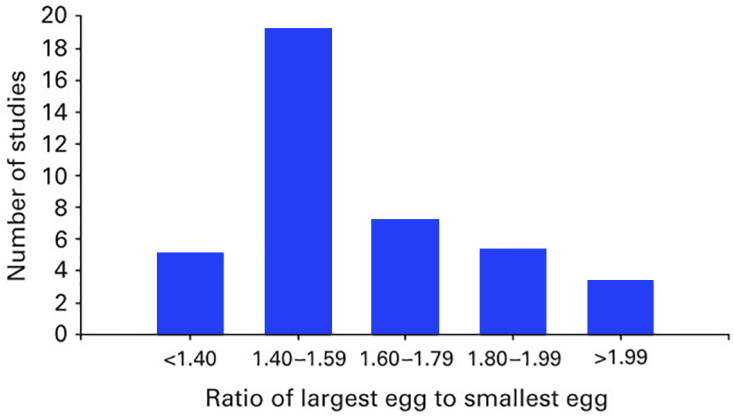

Figure 4.4: The ratio of the size of the largest egg in the population to that of the smallest in 39 studies. From Christians (2002).

Repeatability of estimated fresh egg weight by females was high, indicating that much of the variation in egg weight is a characteristic trait of individual females rather than being strongly associated with other external factors. The magnitude of repeatability I estimated for this population of North Island brown kiwi appears to be similar to other species such as the Great Tit (R = 0.66), Pied Flycatcher (R = 0.61), and Mallard (R = 0.62) (Christians 2002). This high degree of repeatability may warrant further investigation as to the heritability (proportion of phenotypic variation due to additive genetic variation) of fresh egg weight size, which I was not able to do without genetic data.

The selected set of models (Table 4.3) indicate that male body weight, female body weight, and site are important predictors of fresh egg weight, whilst clutch size, male bill length, and sequence of egg in year are less important predictors. The top ranked model of these also happened to be the most parsimonious, containing only male body weight, female body weight and site.

The table of explanatory variable importance (Table 4.4), indicates that male and female body weight, and site are all equally important in explaining estimated fresh egg weight. These three variables were contained in every selected model, and the importance statistic indicates a high degree of certainty that these variables would be contained within the true best model. The other three variables (clutch size, male bill length, and sequence of egg in year) were included or excluded in various combinations from all the models other than the top ranked model. It is however important to note

that the selected models were selected under the very stringent rule of $\Delta AICc < 1$, so all should be considered useful models in predicting fresh egg weight as the relative differences in $AICc$ were very small.

The averaged model (Table 4.5) represents a very useful tool in predicting fresh egg weight, as it takes weighted inference from a range of good models. This means that its parameter estimates were relatively stable compared to if a single model had been chosen (commonly the top ranked model by some statistic such as AIC or R^2). Burnham and Anderson (2002) warned that single-model inference from a linear regression like mine would be susceptible to unstable parameter estimation if new datasets generated by the same underlying processes were re-analysed, which is why I have opted to utilise multi-modal inference.

The fitted values of my averaged model (Figure 4.2) indicated that male body weight had a positive effect on fresh egg weight. Large males were expected to parent large eggs. Male body size influence on egg size has been proposed to be important in sexually dimorphic species (Cabana et al. 1982; Weatherhead & Teather 1994). It may seem counter-intuitive that male size could have an influence, if it is assumed that egg size allometry is purely a consequence of egg production and transportation by the female, but previous studies (Cabana et al. 1982; Weatherhead & Teather 1994) have suggested that males of sexually dimorphic species have an epistatic effect on egg size. This would cause egg size to evolve as a function of both male and female body size. The mechanism that may enable male body size to have an effect on egg size is through female choice of partner (sexual selection) in relation to perceived incubation ability. Females need their eggs to be well incubated, and incubation ability of males may be associated with body weight, so through differential allocation (Horváthová et al. 2012) females may invest more into eggs (bigger eggs) when paired with attractive males. Evidence of egg investment according to male attractiveness has been found in zebra finches (Bolund et al. 2009) and mallard (Cunningham & Russell 2000).

Female weight had a strong positive association with estimated fresh egg weight, this was an even greater effect than for males. This was unsurprising, as females (being the larger sex) take the majority of the burden of reproduction (Downhower 1976). Their large eggs, sometimes in clutches of up to three, contain a substantial amount of energy: an average egg contains 11.45 kJ/g or 4014 kJ/egg - which is the most energy rich egg known (Calder et al. 1978). Females must gather sufficient reserves during the months

prior to laying and are underweight after the breeding season (Calder & Rowe 1977), unlike other birds which are able to gather energy or resources on a sufficient basis day-to-day during egg synthesis (Perrins 1996). It seems reasonable that the larger the female, the more energy she would be able to store for egg production and thus make larger eggs in a given clutch size.

There were differences in mean fresh egg weight between my four sub-sites. Unfortunately I did not have data quantifying food availability or meteorological data at a sub-population level, which would have been interesting to test, as some studies have shown egg mass varies with ambient temperature, both negatively (Bennion & Warren 1933) and positively (Saino et al. 2004) and positively with resource availability (Hamer et al. 1991; Ardia et al. 2006). The differences that were present in the fitted model data were possibly due to differences in the local vegetation types. It would be interesting to know what caused the differences in fresh egg weight between the sites, although for practitioners selecting sites to manage for kiwi conservation a more important consideration would be predator levels, as the results of Chapter 2 would predict small differences in the lifetime survival due to fresh egg weight differences of this magnitude (see Chapter 5 for further discussion).

The effect of male bill length was in the negative direction, although this was a weak effect. It is interesting that this was in the negative direction, as sexual dimorphism in this population was greatest for bill length (see Chapter 3). Why then were the two measures of male body size acting in different directions? There is not much literature applicable to this situation, because North Island brown kiwi are unusual among avian species in male-only incubation. I propose that selection favours male weight sufficient to incubate large eggs (males need sufficient resource reserves as to not need to leave the egg unincubated for extended periods of time (Hanssen et al. 2002)), but that inter-sexual niche differentiation favours a short male bill to avoid competing with the (longer-billed) female sex. The sex with a lower body weight should have proportionally shorter bills than the larger sex, because kiwi with shorter bills cannot forage as deeply underground or underwater so have less potential access to food (Cunningham & Castro 2011).

Sequence of egg had a very weak positive effect. It was interesting that the influence of egg sequence had a non-negative effect on egg size, as it has been proposed that kiwi females are so depleted after egg laying that males then have to take over incubation. If

laying these large eggs were truly such a burden on females it might be expected that egg size would decrease after laying multiple eggs in a year, this is what I found, but the effects were very small (~1 g between the first and fifth egg laid in a year). This result has implications for Operation Nest Egg and other kiwi population managers, because it provides evidence that kiwi only produce another egg if they have sufficient resources for it to be large and birds in these intensive breeding programme are not being unduly stressed.

Estimated fresh egg weight decreased a small amount with increasing clutch size. The fitted weight differences between clutch sizes were small (1-egg clutch = 454.52 g, 2-egg clutch = 445.11 g, 3-egg clutch = 435.69 g), so a similar total clutch mass would result from either two clutches of single eggs (909.04 g), or one clutch of two eggs (890.22). The direction of the clutch effect matched general avian life-history theory predictions (Winkler & Wallin 1987) and this direction has been shown in previous studies (Lack 1967; Sinerbo & Licht 1991; Williams 2001), albeit in a much larger magnitude. Interestingly, the direction of the fitted model was the opposite to the results of simply plotting egg weight according to clutch size without taking into account other covariates or the special data structure. The negative relationship is related to the trade-off a female must make in investing resources between varying numbers of young. I hypothesise that increased clutch size in North Island brown kiwi is associated with resource availability both prior to laying (for egg production, relevant to parents) and post-laying (for chicks to easily forage once yolk reserves are depleted). Brown kiwi chicks initially forage close to their nests and feed themselves independently, so having a multiple-egg clutch would increase intrabrood competition. Because lifetime survival is strongly associated with juvenile growth (see Chapter 2), parents would be under strong selection to ensure that their offspring have adequate resources available for growth.

Other factors which were tested but turned out to not be important in predicting fresh egg weight were female bill length, laying date, # nest in year, and # egg in nest. Univariate metrics of avian body size may not be ideal measures of overall body size (Freeman & Jackson 1990). Though I tested interaction terms between weight and bill length for both sexes, these turned out to be non-significant. Using the first principal component from a range of body size metrics (weight, bill length, tarsus width, tarsus depth, tarsus length) may yield a more accurate representation of overall avian body size. The best single metric of avian body size was suggested to be either tarsus length

or mass (Freeman & Jackson 1990), I used mass because it showed the most sexual dimorphism and it had the greatest number of complete records. Laying date was expected to be a significant predictor because kiwi show strong seasonality in egg laying, with two peaks in June-July and October-November. The subsequent peak is much smaller, so a strong tendency was evident.

This Chapter provides important information for understanding egg size variation in North Island brown kiwi. I have presented significant predictors of fresh egg weight, and quantified their magnitude and direction. Most of the predictors were in the expected direction (based off previous literature), even though in many regards kiwi are unusual and do not conform to general avian relationships. Most of the predictors (other than parent body weight) had small to very small effect sizes, and I could find no evidence of important consequences for Operation Nest Egg (which I will cover in more detail in Chapter 5).

5 Synthesis: why is an understanding of egg size in kiwi important?

Kiwi are an iconic New Zealand group of five species, found nowhere else in the world, but they are unfortunately declining in population size and range (Miskelly et al. 2008). Some kiwi species survive exclusively on offshore islands and mainland predator-free reserves (Holzapfel et al. 2008), and, as a result, the majority of New Zealanders will never encounter kiwi in the wild. The decline of kiwi has undoubtedly been anthropogenically induced (Diamond & Veitch 1981; McLennan et al. 1996), and many people feel compelled to save kiwi from extinction (Bennett et al. 2015). There are varied reasons to value biodiversity, but people often recognise moral justifications (Oksanen 1997), monetary benefit from ecosystem services (Dumont 2005; Baumgartner 2008), cultural or spiritual reasons (Sani 2002), and legal responsibilities. Additionally, kiwi are an "umbrella" species (see Roberge & Angelstam 2004 for definition), thus activities which help kiwi also help a range of other species (Cullen et al. 2005; Joseph et al. 2009). For example, kiwi are sensitive to predation so sites that contain kiwi are often prioritised for pest eradication, which in turn benefits other fauna and flora in the same area (Cullen et al. 2005).

5.1 Relevance of site selection

Conservation managers have limited budgets so selection criteria must be used to prioritise suitable areas for potential management (Coppolillo et al. 2004; Margules & Sarkar 2007). In Chapter 2, I described a methodology for estimating the number of days a chick spent at risk under 800 g, and the probability of reaching 800 g. In Chapter 4, I estimated the differences in fresh egg weight due to differences between my four sub-sites. Here I combine these two methodologies to estimate the importance that site may have in kiwi fitness (Table 5.1).

Table 5.1: Estimated survival differences for North Island brown kiwi according to fitted values for sites in Rarewarewa Reserve, Northland. Site abbreviations: Purua (P), Riponui (Rp), Rarewarewa (Rr), and Hodge's Bush (H).

Site	Mean fresh egg weight (g)	Estimated chick weight	Days to 800 g	P(reaching 800 g)
P	461	355	111.43	0.51
Rp	476	367	108.44	0.52
Rr	425	327	118.55	0.5
H	445	342	114.54	0.51

These results indicate that the probability of reaching 800 g is very similar between all the sites. For practitioners selecting new sites for kiwi conservation, concerns around suitability of habitat should come second to predator levels or the ability to defend the site against predators. The sites in my study varied in their vegetation (including native bush, farmland pasture, plantation pine forest), but these probabilities were similar. Conversely, predation has a large effect on the fitness of kiwi and should be a top priority. However, note that these are estimated survival probabilities based on the small differences in egg weight; actual survival may be affected by many other factors which differ between sites.

5.2 Implications for Operation Nest Egg

One of the most successful tools the Department of Conservation has for managing kiwi populations is Operation Nest Egg (ONE) (see Chapter 1 for details). ONE has seen targeted populations stop declining and in many cases increase in size and/or range. Another benefit of ONE has been the reintroduction of kiwi back into areas that had previously been decimated (Colbourne et al. 2005; Harper & Brown 2014). Having a more diverse range of source populations reduces inbreeding depression and improves security of species as a whole (Frankham 1995). ONE has been so successful that it now includes other kiwi species (rowi *Apteryx rowi*) and recently whio *Hymenolaimus malacorhynchos* (program name: WHIONE). Knowledge and techniques developed in

one species certainly would have had benefit in applying the programme to other new species.

A key tenet of ONE is that when they take eggs from a wild nest, the parents often lay replacement clutches (Colbourne et al. 2005). This increases the reproductive output (number of eggs in a year) of parents, but there are concerns that if egg production is costly for parents then ONE may be harming those birds that repeatedly have their eggs taken away. If this was the case, it would be reasonable to expect to see a decline in egg size where multiple eggs are laid in a season due to the physiological stress parents might be under. The results of this thesis culminated in Chapter 4, which examined what factors influence egg weight of North Island brown kiwi. This chapter did provide many significant and interesting results (such as the strong association with parental body weight), but possibly even more interesting were some of the factors which were tested but found not to be significant; that egg size is not associated with the number of eggs that parents lay in a year, or the number of eggs in a clutch, or the order of eggs in a clutch. These results are even more striking when considering that the kiwi in this study had increased yearly egg production (due to being in ONE) compared to other kiwi populations, and still showed no significant trends across these metrics. I believe that non-significant variance in egg weight was found because females are not forced to lay additional eggs, and my data clearly shows that female kiwi do not produce additional eggs if they are not going to be large.

The methodologies developed in this thesis could also be used to determine if parent rowi or whio are being negatively affected due to having their eggs taken over extended periods of time. I would recommend measuring similar variables for a model predicting fresh egg weight, in addition to female weight and survival over time. In determining whether parents are being stressed due to their reproductive outputs, a metric such as fresh egg weight (otherwise egg volume) should be examined in addition to parent body weight or condition. Parents may adaptively lose body weight during the breeding season only to re-gain condition before the next season (Williams 2005), and year-to-year resource variability may confound the ability to detect stress on parents.

Female kiwi varied greatly in mean fresh weight of their eggs, and this variation was much greater than of all the other explanatory factors combined (compare the R^2_m with the R^2_c in Table 4.3). This could have implications if ONE wanted to increase the average size of eggs resulting from their programme (which would be an admirable

goal considering egg size is positively associated with fitness), as it seems likely that some genetic component controls for egg size in North Island brown kiwi. However, such selective breeding of a rare species should be undertaken with extreme care (Miller 1995). The slight additional fitness benefits from increasing the average size of juvenile kiwi could possibly be outweighed by the negative fitness consequences of reducing the genetic diversity of the species by selectively breeding (Frankham 1995). Additionally, variation in egg size could be adaptive (plasticity) in order to cope with environmental stochasticity altering optimal egg size (Crump 1981; Kaplan & Cooper 1984; Allen et al. 2008). For these reasons, I would advise against the results of this thesis being justification for selective breeding of North Island brown kiwi to increase average egg or juvenile size.

5.3 Final remarks and future directions

Notwithstanding the contributions of this thesis, there is much still to be learnt about the breeding ecology of North Island brown kiwi. To build on my results, I hope that future researchers will be able to gather new data from more natural-like kiwi populations to act as a reference. Additionally, if individual kiwi were to be followed over their lifetimes, it would be possible to identify if kiwi make trade-offs between lifespan and egg production. This has primarily been an ecological study, and, as such, limitations to identifying possible causal mechanisms are inherent; genetic research will resolve many of the questions surrounding the heritability of egg size in North Island brown kiwi, and physiological research will better quantify the potential stress suffered by parent kiwi subject to artificially increased reproductive output.

Further scope for research could involve conducting supplementary feeding experiments to assess constraints on egg size in kiwi, as has been done in overseas studies (see Chapter 1). The Department of Conservation is already well versed in supplementary feeding of other threatened bird species, and captive kiwi managers follow best practice guidelines for feeding based on kiwi dietary requirements, so this sort of experiment could be simple to setup (possibly utilising the large number of captive kiwi in New Zealand and around the world). Also, it would be interesting to further examine the costs associated with incubating large eggs for male parent kiwi. This could be performed within and/or between species, as different kiwi species vary in both mean egg size and in their share of incubation duties. The male-only incubation of North

Island brown kiwi is considered to be of more recent origin than the shared incubation of rowi (*Apteryx rowi*), and tokoeka (*Apteryx australis*) (Colbourne 2002). Some tokoeka have been observed having so many incubation 'helpers', of both sexes, that the male parent ends up doing no incubation themselves (Colbourne 2002).

This thesis has contributed to the evolutionary and physiological understanding of North Island brown kiwi, in addition to having conservation implications for the species and Operation Nest Egg. This has been achieved firstly by having access to an unprecedentedly large dataset on kiwi reproductive characteristics. Previous studies of wild kiwi breeding ecology have been small ($\leq$ 30 nests), over short time spans ($\leq$ 3 years) mainly due to the high risk of nest desertion (kiwi are long-lived with many future breeding opportunites so should not risk any current reproductive season for numerous future ones). This study was less concerned with nest desertion due to the eggs being taken away for incubation anyway. Secondly, the use of recently developed statistical tools has allowed for greater insights into these data not previously possible. Mixed effects models in particular, and the related goodness-of-fit methodology for mixed effects models (developed by Nakagawa & Schielzeth (2013)) have been critical for this thesis. These statistical tools have become accessible due to the open source statistical programming language `R`.

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